The Origin of Prosociality Toward Strangers

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
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ABSTRACT

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Abstract

Humans are champions of prosociality. Across different cultures and early in life, humans routinely engage in prosocial behaviors that benefit others. Perhaps most strikingly, humans are even prosocial toward strangers (i.e. xenophilic). This is an evolutionary puzzle because it cannot be explained by kinship theory, reciprocal altruism or reputation. The parochialism hypothesis proposes that this extreme prosociality is unique to humans, is motivated by unselfish motivation and evolved through group selection made possible by human culture and warfare. The first impression hypothesis, on the other hand, proposes that xenophilia can evolve to promote the selfish benefits that accrue from extending one's social network. It predicts that 1) nonhuman species can evolve prosociality toward strangers when the benefit of forming new relations is higher than the cost, 2) the motivation for prosociality can be selfish, and 3) encounters with strangers can be a positive social event since strangers represent potential social partners. This dissertation presents three sets of experiments designed to test these predictions with bonobos (*Pan paniscus*), a species known for reduced xenophobia. These experiments showed, first, that bonobos voluntarily shared monopolizable food with a stranger and helped the stranger to obtain out-of-reach food. Second, the observed prosociality was driven by a selfish motivation to initiate an interaction with the stranger in close proximity and an other-regarding motivation to

benefit the stranger. Third, an involuntary yawning task and a voluntary choice task show converging results that bonobos attribute positive valence to completely unknown strangers by default. These experiments support the three core predictions of the first impression hypothesis and challenge the view that intergroup competition is crucial to the origin of prosociality toward strangers in our species. Instead, the first impression hypothesis proposes that xenophilia in bonobos is probably an adaptation to initiating non-kin cooperation. Because female bonobos are highly cooperative even though they are the dispersing sex, xenophilia might function to quickly establish cooperative relationships with new immigrants. This suggests that xenophilia and reciprocity are likely two complementary aspects of non-kin cooperation: the former explains its initiation while the latter explains its maintenance. Similarly, xenophilia in humans is likely a result of the increasing need for cooperation among non-kin due to enhanced fission-fusion dynamics, population expansion, obligate cooperative foraging and greater dependence on cultural knowledge.

Dedication

To my grandfather.

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Acknowledgements

I am deeply grateful to my advisor Dr. Brian Hare. I could not have found an advisor whose interests and passion match so perfectly with my own. I will never forget those moments spent drawing study designs on a white board, on a piece of scratch paper, on the floor right outside the bonobo building, or even in complete darkness after the power went out. We were so excited. And I call them little-kids-standing-in-front-of-a-room-full-of-candies moments. Working with you is not only exciting but also electrifying. It remains a mystery where your charging station is, but you seem to have unlimited positive energy (and standby hours). I honestly think there is nothing you cannot see the bright side of (well, Pepsi maybe). You showed me the genuine, undistracted curiosity needed to just "figure it out". You taught me by example how to blend this idealistic passion with realistic thinking. You gave advice that was always in my best interest. You… Thank you Brian. You are the best mentor a graduate student could possibly ask for.

I am thankful to Dr. Steve Churchill. You are a wonderful mentor who has been so patient with a student who does not know a lot about anatomy and hunter-gatherers. And you have the charisma to turn these topics into a lot of fun. I still remember what you said when you were giving the EATS talk about sediba: "These questions keep me up at night". I am very grateful to Dr. Lasana Harris. Working with you is always relaxing and encouraging. From running human subjects to discussing nuanced details

about neuroscience, you were always there to help, no matter how busy or how trivial my question. Also thank you Dr. Dan Ariely. I learned so much from your class and from discussion with you in committee meetings. I particularly appreciate your generous help and insight regarding my career development. I am also grateful to Dr. Anne Pusey. You gave me numerous much needed comments and pointed out the importance of scrutinizing fieldwork data.

I want to thank my college advisor Dr. Yanjie Su. You have my utmost respect because when I was an undergrad you were the only Chinese professor who was doing animal cognition research. Your persistence made my career possible. I also want to thank Dr. Stephen Stearns for writing me a recommendation letter that changed my life five years ago. I was also so lucky to join your seminar in your only semester in China. That seminar was my first exposure to evolutionary thinking of human behaviors. A lot of the class readings are cited in this dissertation. Finally, I am deeply grateful to Lijing Peng. We are not siblings but we are as close as any brother and sister. You have the magic to always believe that there is a brighter side to everything, and your warmth can break the coldest ice. Thank you for showing me *The Dead Poets Society* at the critical moment when I had to decide whether I should choose this risky career path.

I am grateful to Evan MacLean. I am an only child, but if I were to have a big brother, Evan would be the one. Your kindness and supportiveness break every stereotype that Asians are generally nicer than Americans. I really had a good time

sharing an office with you for five years and spending two Congo trips together. I am thankful to Chris Krupenye. If I were to have a little brother, Chris would be the one. Your kindness might again break every stereotype that Asians are generally nicer than Americans. But it is your relentless passion about science that constantly reminds me of how invaluable youth is (and how little I have left). I want to thank Kara Schroepfer. Testing 300 dogs over the span of three years would not be possible without you keeping everything organized. Also, I would never have returned from Congo with so much data were it not for your French translation, explaining to the keepers that it was not "I have finished all the bonobos" but "I have finished all the bananas". Also, thank you Alex Rosati and Tory Wobber for being so smart and giving me so much constructive advice. I want to thank Korrina Duffy, Rachna Reddy, Kara Leimberger, Alyx Reinhardt, Judy Songrady and Beatrice Capestany for keeping my life organized. I am very thankful to Karen McCall for her constant encouragement and the dissertation care package. Lastly I am grateful to Heather Mann for telling me there is a thing called work-life balance. Thank you for being a funny and wonderful writing buddy in my most imbalanced days.

I am incredibly thankful to Claudine André, Dominique Morel, Valery Dhanani, Debbie Cox and Rebecca Atencia for welcoming me to work in the sanctuaries. Special thanks to Claudine. You are a true inspiration. You show me the most beautiful things can be grown in the most broken places. Also thank you Suzy Kwetuenda. You are also

an inspiration (and a born comedian). I still remember trying really hard to convince you that you were crazy. “A Congolese woman studying bonobos just because you love it? And you are even the first Congolese ever to study bonobos? You are crazy! But in a good way, one of a kind!” I am very thankful to the staff at Lola ya Bonobo, not only for their help but also for their cheerful spirit. Each year I had the best time when I was in the field.

Finally, I cannot be more thankful to my dad, my mom, my grandparents and my family in China. No matter how much humans are nice to strangers, unconditional love is always flowing from family. It is already incredibly difficult to tolerate their only child being thousands of miles away. It is even more difficult to allow him to pursue a career that no Chinese has ever done before, hide their worries and continue to encourage him. I am just so lucky to be part of this family. Thank you.

1. Why be nice to strangers: the parochialism and the first impression hypothesis

Humans are ultra-cooperative: our species cooperates in a myriad of fashions that involve multiple participants with various roles (Tomasello 2009). Moreover, humans frequently cooperate with unrelated individuals – including those that are completely unfamiliar (Seabright 2004, Sterelny 2012). This can even include forms of costly cooperation in which an actor behaves to benefit an unrelated and unfamiliar recipient at a cost to themselves (Fehr & Fischbacher 2003).

Observational and experimental work suggests that such tendencies are a robust and perhaps universal psychological trait in humans (Henrich et al. 2005, 2006, 2010). This would seem to pose a challenge for traditional explanations of cooperative behavior (i.e. kinship theory and reciprocity) leading many to suggest that our species may have evolved a unique propensity for cooperation that is the root of what makes our species unique (Tomasello 2009, Fehr & Fischbacher 2003, Hill et al. 2009). Does this ultra-cooperativeness make us human? Guided by this question, my dissertation research will consist of three sets of experiments designed to answer the question: What are the phylogenetic and functional origins of our species' prosocial preferences toward strangers?

1.1 Background

Prosociality was initially defined by developmental and social psychologists to include behaviors where an actor voluntarily benefits a recipient even if for selfish ends (see Eisenberg et al. 2006, Fehr et al. 2008, Jaeggi et al. 2010a, Vaish & Warneken 2011, Cronin 2012, House et al. 2012). This is to be contrasted with forms of antisocial behavior in which an actor behaves aggressively or with frustration towards a recipient in the same context (Wispé, 1972).

Although human cooperation might be special because of our complex cognitive abilities that include skills such as low discounting rates, inhibitory control, planning and sophisticated theory of mind (Stevens & Hauser 2004, Tomasello et al. 2005), the most puzzling human cooperative phenomenon from an evolutionary perspective is our species' prosocial behavior toward unfamiliar, unrelated individuals (Seabright 2004). Spontaneous helping and costly donation to strangers have been consistently observed in natural and laboratory settings cross-culturally (Camerer 2003, Fehr & Fischbacher 2003, Henrich et al. 2005, Levine et al. 2001). Prosociality toward strangers emerges in early infancy (Warneken & Tomasello 2006) and is partially heritable (Cesarini et al. 2008). Prosociality is even observed in anonymous, one-shot interactions with strangers for which selfish benefits such as reciprocal exchange and reputation cannot account. Therefore, it has been suggested that our prosocial behavior is driven by unselfish motivations or other-regarding preferences in which choices are driven by concern for the welfare of others (Fehr & Fischbacher 2003, Silk et al. 2005). Given that helping

unfamiliar individuals cannot be explained by kinship theory (Hamilton 1964), reciprocal altruism (Trivers 1971) or potentially even reputational effects (Nowak & Sigmund 2005), the origin of this pro-sociality remains a mystery and is considered as one of the big challenges to evolutionary theory (Williams 2009).

Table 1 Summary of the parochialism and the first impression hypothesis

		The parochialism hypothesis (the null hypothesis)	The first impression hypothesis (the target hypothesis)
Pro-sociality towards strangers	Function	Intergroup competition	Extension of individual social network
	Phylogeny	Unique to human, evolving via group selection maintained by human culture and warfare	Not unique to human, evolving when the benefits of forming new relationships outweigh its costs and risks
	Prosocial motivation	Unselfish motivation	Selfish and unselfish motivations
	Appraisal of strangers	Strangers from ingroup = friends, strangers from outgroup = foes (i.e. ingroup love, outgroup hate)	Strangers = potential new partners (i.e. positive valence by default)

1.2 The parochialism hypothesis

The parochialism hypothesis proposes that the prosociality observed in humans is the result of our species' culturally determined social norms (Table 1). This hypothesis also suggests that our species' prosocial tendencies could only have evolved as a result of group selection (Gintis et al. 2003). According to this hypothesis, the self-detrimental effect of the prosocial act (West et al, 2007) can only be explained as an evolutionarily stable strategy if culture and warfare create and maintain sufficient heterogeneity

among social groups to enable competition at the group level (Boyd & Richerson 2009, Choi et al. 2007). As a result, our exceptional prosociality evolved as an adaptation to this intergroup competition because cooperative strangers contribute to the average competitiveness of the actor's group (Fehr & Fischbacher 2005, Richerson & Boyd 2005).

Consistent with this hypothesis, human prosocial behavior is usually biased towards in-group members with subjects tending to help, protect and share resources with members of an in-group over an out-group (Hein et al. 2010, Levine et al. 2005, Stürmer et al. 2005, Bernhard et al. 2006, Fehr et al. 2008). Moreover, exogenous administration of oxytocin promotes cooperation with unknown strangers (Kosfeld et al. 2005, Zak et al. 2007), but not if the cooperative partner is a stranger from a known out-group (De Dreu et al. 2010). The parochialism hypothesis, also has a strong phylogenetic prediction that has received initial support: pro-social behavior directed toward strangers should be a derived feature of human psychological evolution (i.e. nonhuman apes do not have high enough cultural fidelity or sufficient between group competition to drive the evolution of social norms that maintain pro-sociality in humans). Studies with nonhuman primates, and in particular chimpanzees (*Pan troglodytes*), suggest that pro-social behavior observed in nonhuman apes are largely the result of harassment as opposed to active or voluntary food-sharing (Stevens 2004, Gilby 2006, Silk et al. 2005, 2013, Jensen et al. 2006, Vonk et al. 2008, Yamamoto & Tanaka 2009). Even when chimpanzees exhibit spontaneous pro-social behavior it is only directed toward familiar

conspecifics (Warneken et al. 2007, Yamamoto et al. 2009, Greenberg et al. 2010, Melis et al. 2010).

Three lines of evidence have recently presented a challenge to the parochialism hypothesis. The phylogenetic prediction that pro-sociality toward strangers is unique to humans is inconsistent with the finding that bonobos (*Pan paniscus*) are capable of voluntarily sharing monopolizable food with conspecific recipients (Hare & Kwetuenda 2010). Critically, subjects had the strongest tendency to share when paired with an unfamiliar recipient, indicating bonobos may direct pro-social behavior toward strangers. The motivation prediction of the parochialism hypothesis is also challenged. An increasing number of studies have demonstrated that even when humans are placed in an anonymous, one-shot interaction, they likely remain highly sensitive to implicit cues of reputation (Burnham & Hare 2007, Haley & Fessler 2005, Hoffman et al. 1996). These findings have led some researchers to argue that the seemingly unselfish behaviors observed in many economic experiments are actually the result of selfish motivations. According to this mismatch hypothesis (Boyd & Richerson 2002, Burnham & Hare 2007), human foragers infrequently experience anonymity in normal social interactions. This mismatch between normal social interactions and experimental settings causes misfiring of proximate mechanisms driven by selfish motivation and shaped to enhance one's reputation (Burnham & Johnson 2005, Levitt & List 2007). Finally, the appraisal prediction of the parochialism hypothesis is also challenged.

Although the parochialism hypothesis predicts intergroup bias, it provides no explanation to why humans are consistently helpful and generous to strangers without knowing their social membership (cf. Camerer 2003). Few studies have tested whether humans treat strangers of known group membership and strangers of unknown group membership differently. Moore (2009) found that in certain contexts, young children would behave pro-socially toward both a friend at the same school and a strange peer from a different school but not a non-friend groupmate. Both of these findings suggest that humans are not simply directing pro-social behaviors toward group-mates to the exclusion of all others, as suggested by the parochialism hypothesis. Instead, these findings point to the likelihood that humans behave pro-socially toward strangers *by default*, and their basal motivation is to extend their own personal social network.

1.3 The first impression hypothesis

The first impression hypothesis presents an alternative explanation for the origin of human prosociality toward strangers. In contrast to the parochialism hypothesis, the first impression hypothesis proposes that human prosociality toward strangers evolved because the benefits of extending one's own personal social network outweigh the costs and risks of forming a new social relationship. The central idea is that prosociality toward strangers will be favored when the costs of inter-group interactions are low, allowing individual selection to promote the expansion of an actor's social network due to the benefits of sociality (Table 1).

The costs of a new social relationship can be significant. First, initiating an interaction with strangers can be highly risky in species engaged in intergroup violence (Wrangham 1999). Social life also intensifies competition over resources and increases vulnerability to diseases (Altizer et al. 2003, Janson & Goldsmith 1995, Kappeler & van Schaik 2002). Nevertheless, given the prevalence of sociality among primates and other animals these costs must often be overcome by the potential benefits of social life (cf. Silk 2007). The potential benefits for an individual in expanding its social network include inbreeding avoidance (Pusey & Wolf 1996), predation avoidance (van Schaik 1983), territory defense (Crofoot & Wrangham 2010, Wrangham 1980), stress reduction (Abbott et al. 2003, Engh et al. 2006, Sapolsky 2005, Taylor et al. 2000), offspring care (Clutton-Brock 2002, Kokko et al. 2001), cooperation (Melis et al. 2006b, Hare et al. 2007), and commodity trading (Noë & Hammerstein 1994). Therefore, when the costs of social life are diminished and/or the benefits of sociality become overwhelming, pro-sociality toward strangers should be favored by natural selection at the level of the individual. This scenario seems particularly plausible in the case of humans where the benefits of sociality are so extreme: human foragers live in highly interconnected population with a high proportion of non-kin, show unmatched social cognition, engage in obligate cooperation on a daily basis and depend on cumulative cultural knowledge that can be shared within and between generations (Foley & Gamble, 2009, Herrmann et al. 2007, Hill et al. 2009, 2011, Powell et al. 2009, Sterelny 2011).

Providing initial phylogenetic support of the first impression hypothesis is the fact that chimpanzees (*Pan troglodytes*) do not show pro-social tendencies toward strangers. The cost of encounters with strangers can be extreme, given that lethal intergroup aggression is one of the leading causes of mortality in adult chimpanzees (Williams et al. 2008). As a result, chimpanzees are sensitive and highly averse to the risks associated with inter-group encounters (Emery Thompson et al. 2007, Mitani & Watts 2005, Wilson et al. 2001, 2007). Moreover, intense feeding competition causes strong aversion to new immigrants, which sometimes leads to fatalities (Kahlenberg et al. 2008, Pusey et al. 2008, Townsend et al. 2007, Williams et al. 2004). Expansion of an individual's social network through interactions with strangers is thus too expensive for chimpanzees, and it is not surprising that even though they are helpful, little prosociality to unfamiliar individuals has been observed in the wild (except for the purpose of mating, Kahlenberg et al. 2008).

Given the potential benefits to an individual of expanding its social network when the risks of such interactions are low, the first impression hypothesis has three core predictions:

- The phylogeny prediction: prosociality toward strangers will be present in nonhuman social species with high-levels of social tolerance and low risk of intergroup aggression.
- The motivation prediction: prosociality toward strangers can be a result of

selfish social motivations and does not necessitate unselfish motivations.

- The appraisal prediction: strangers should have a positive valence and be perceived as potential new partners. The first encounter between strangers should generate a positive appraisal unless clear information suggests that they are unlikely to become partners (i.e. aggressive disposition, out-group status, etc.).

These core predictions of the first impression hypothesis will be examined in the following chapter by studying bonobos.

1.4 Bonobos provide a powerful test of the two hypotheses

Bonobos are an ideal species to examine the first impression hypothesis, because the costs associated with inter-group competition are unusually low. In stark contrast to chimpanzee, border patrols, infanticide and lethal intergroup aggression have never been observed in captive or wild bonobos (cf. Hare et al. 2012, Wrangham 1999). Though tension can arise during intergroup encounters, they are usually no more than vocal displays and rarely escalate into physical fights (Badrian & Badrian 1984, Hohmann & Fruth 2002, Kano 1992, Myers-Thompson 2002). Moreover, unlike chimpanzees, intergroup interactions can even result in amicable social interactions that involve grooming, socio-sexual and play behavior between adults (Furuichi 2011). Bonobos are reported to live in more stable parties, with a higher number and proportion of females in foraging parties (Furuichi 2011). Bonobos are believed to display higher co-feeding tolerance than chimpanzees because bonobos evolved in a rich, gorilla-free habitat that

reduced feeding competition (Hare et al. 2007, Kuroda 1979, Malenky and Wrangham 1994, Paoli 2009, White 1992, Wobber et al. 2010a, Wrangham & Peterson 1996, but see Jaeggi et al. 2010b, Hohmann et al. 2010). Consistent with the notion of more affordable sociality, affiliative rather than agonistic behaviors characterize immigration events of females in the wild (Idani 1991, Furuichi 2011). In corroboration, captive bonobos, regardless of sex or age, can be introduced with relative ease. Even two long-separated groups with multiple adult males can be reintegrated in absence of physical contact aggression (Gold 2001, Pfalzer & Ehret 1995, Holt & van Elsacke 1990).

1.5 Rationale of this dissertation research

Three main sets of experiments were conducted to examine each core prediction of the first impression hypothesis. First, to test the phylogenetic prediction, a series of food-sharing experiments were conducted to test whether bonobos exhibit pro-social preferences toward strangers. A second set of experiments tested the prediction that pro-sociality toward strangers could be selfishly motivated by examining the proximate motivation of the pro-social sharing observed in bonobos. Finally, a third set of experiments was conducted to test the appraisal prediction that bonobos will by default attach positive valence to strangers.

1.5.1 Study 1-2: Are bonobos prosocial toward stranger? If so, what are the motivations?

This chapter addresses the phylogenetic prediction and the motivation prediction

together. First, two food-sharing experiments examine whether bonobos pro-socially share monopolizable food with a conspecific, and if they do, whom they will prefer to share with, a groupmate or a stranger. These experiments employ the paradigm developed by Hare and Kwetuenda (2010), wherein a subject bonobo enters a room with a pile of highly desirable food and could share it by removing a wooden key to release recipients locked in adjacent rooms. Given that the subject has complete control over the food, releasing a recipient to eat together is voluntary and pro-social. However, selfish motivation can drive prosocial behavior in this paradigm because the subjects gain potential social rewards by releasing a social companion into close proximity.

The second set of four experiments examine whether prosociality toward strangers is driven by unselfish motivations. Unlike the first two food-sharing experiments where the actors can obtain potential social reward by interacting with the recipient, these experiments are designed to remove these potential, selfish benefits. If the actors remain prosocial, then their prosociality is motivated by unselfish concerns for others' welfare (or other-regarding preference). If the actors stop being prosocial, then their prosocial motivation is selfish.

Previous studies on other-regarding preference in non-human primates have primarily relied on two types of paradigms, prosocial choice and instrumental helping. First, inspired by the dictator game utilized in human studies, the prosocial choice paradigm allows an actor to choose between 1) a pro-social option that rewards both self

and a recipient and 2) a selfish option that is self-rewarding only (e.g. Jensen et al. 2006, Silk et al. 2005). Of importance is that the actor and the recipient do not need to stay in the same room, because an apparatus or an experimenter will deliver the rewards directly into separate testing rooms. Moreover, the payoff matrix of the two options can be manipulated such that the costs of the pro-social behavior are measurable and controllable. Second, the instrumental helping paradigm places an actor into a context wherein a recipient needs help to gain access to out-of-reach items. Instead of donating goods, the actor behaves pro-socially by providing service (e.g. removing a wooden peg), which arguably is a more naturalistic behavior (Warneken & Tomasello 2009). Similar to the prosocial choice paradigm, the actor and the recipient are separated during the test, restricting the potential for social contact. Both paradigms have been administrated to several primate species (the prosocial choice paradigm: chimpanzee: Jensen et al. 2006, Silk et al. 2005, Vonk et al. 2008; marmoset: Burkart et al. 2007; capuchin: Lakashminarayanan & Santos 2008; the instrumental helping paradigm: chimpanzee: Greenberg et al. 2010, Melis et al. 2010, Warneken & Tomasello 2006, Warneken et al. 2007, Yamamoto et al. 2009; macaques: Massen et al. 2010, 2011; capuchin: Barnes et al. 2008); however, these studies are limited in scope because bonobos have never been tested, all recipients were familiar, and the pro-social behavior was rarely costly to the subjects. For instance, in all of the prosocial choice tests, the subject's payoff remained identical in the pro-social and the selfish option; in most of the

instrumental helping tests, helping neither required a significant amount of effort nor caused loss of desirable items (but see Melis et al. 2006b).

These second set of experiments are designed such that 1) they limit the social contact between the actor and the recipient to minimize immediate benefits of the pro-social act; 2) they allow no role reversal during the test period to prevent reciprocal exchange; 3) they employ two widely-used paradigms to encompass all possible contexts to detect pro-social behaviors; 4) they vary in the costs of pro-social behavior, with some conditions cost-free and the others costly.

In two instrumental helping experiments, a recipient is locked in a room by a wooden key and a pile of food is placed outside that room. The key is attached to a long rope and a subject in another room can help the recipient by pulling it to remove the key. In low-cost helping experiments, the subject has no access to the food so helping is relatively cost-free; while in the high-cost experiment, the food can be consumed by the subject and thus will be lost upon the release of the recipient. In two prosocial choice experiments, a subject chooses between two options, one pro-social and the other asocial. In the no-cost sharing experiment, choosing the pro-social option donates one piece of food to a recipient and one piece to the subject (1/1); while the asocial option only brings the subject a piece of food (1/0). In the costly sharing experiment, the asocial option brings the subject two pieces (2/0), but the pro-social option donates one to the subject and three to the recipient (1/3).

The parochialism hypothesis predicts that 1) bonobos will not be prosocial toward strangers because they do not have human-like culture and warfare, and 2) prosociality toward strangers, if any, must be motivated by other-regarding preferences. The first impression hypothesis predicts that 1) bonobos will be prosocial toward strangers at least in some contexts due to a lack of intergroup aggression and relatively relaxed feeding competition, and 2) prosociality toward strangers can be driven by both selfish motivations to initiate a new social relationship and other-regarding motivation to benefit others.

These experiments will be organized into two separate studies. Study 1 includes the two food-sharing experiments and the two instrumental helping experiments. Study 2 reports the two prosocial choice experiments.

1.5.2 Study 3: Do bonobos attach positive valence to strangers?

As reviewed above, the first impression hypothesis proposes that pro-social behavior functions as a recruitment of potential new partners. Therefore, bonobos should have a positive appraisal of the encounters with strangers and strangers should create positive valence by default. This positive appraisal is proposed as the first step of establishing a new social bond, because it allows unfamiliar individuals to engage in peaceful interactions in close proximity (Carter & Porges 2010). Study 3 examines this appraisal prediction by testing whether bonobos, by default, have positive valence toward unfamiliar conspecifics. Two different paradigms are used to measure the valence: the

contagious yawning task and the social valuation task.

Contagious yawning refers to an increased propensity to yawn after a visual or an auditory exposure to others' yawns (Provine 1996). This contagion is involuntary and is presumably governed by an involuntary process that synchronizes the emotional states of self and others (emotional contagion, Preston & de Waal 2002, Decety & Svetlova 2012). Recent studies have confirmed that this phenomenon might be widespread in the animal kingdom (human: Provine 1986, Platek et al. 2003, Norsica & Palagi 2011; bonobo: Demuru & Palagi 2012; chimpanzee: Anderson et al. 2004, Campbell et al. 2009, Campbell & de Waal 2011, Massen et al. 2012; gelada baboon: Palagi et al. 2009; stumptail macaque: Paukner & Anderson 2006; dog: Joly-Mascheroni et al. 2008, Harr et al. 2009, O'Hare & Reeve 2011, Silva et al. 2012). Both the ultimate benefit and the proximate mechanism of contagious yawning remain unclear (Yoon & Tennie 2010, Guggisberg et al. 2010, Gallup 2011). However, it is evident that contagious yawning is a reliable indicator of a positive social relationship. In several primate species including humans and bonobos, contagious yawning has a stronger effect when the yawner has a closer bond with the observer (Palagi et al. 2009, Norscia & Palagi 2011, Demuru & Palagi 2012, but see Massen et al. 2012). Campbell and de Waal (2011) demonstrated that chimpanzees show contagious yawning after viewing the yawns of familiar groupmates but not unfamiliar outgroups. Given the strong hostility towards unfamiliar chimpanzees (Muller & Mitani 2005; Wilson & Wrangham 2003), this finding suggests

that contagious yawning can also be a measure of default appraisal of strangers. Following Campbell and colleagues, a yawning experiment examines if bonobos yawn contagiously with strangers.

Lastly, in the social valuation task the subjects can choose between two options of different values. The value of one option is always known and contains a fixed amount of food reward. However, the value of the other option is variable. This second option usually contains some reward plus different type of social stimuli. The subjects' valuation of various stimuli can thus be measured by comparing their relative preferences between the two options. For instance, both macaques and humans attribute higher values to visual stimuli important to survival and reproduction and are willing to pay a higher cost to watch these stimuli (Aharon et al. 2001, Deaner et al. 2005, Hayden et al. 2007). In the current version of the social valuation task, the subjects can choose between a small, immediate reward and a large, delayed reward (Rosati et al. 2007; Rosati & Hare, 2013). When the subjects are waiting for the delayed reward, they are shown either videos of strangers or videos of groupmates. The subjects should be more willing to choose the delayed reward if they attribute a positive valence to strangers.

According to the parochialism hypothesis, outgroups will be associated with negative valence (i.e. xenophobia). This hypothesis predicts that 1) contagious yawning will be absent among strangers and 2) in the social valuation task the videos of strangers will decrease the value of the delayed reward. According to the first impression

hypothesis, strangers are potential new partners so they will 1) trigger contagious yawning and 2) increase the value of the delayed option in the social valuation task.

2. Empirical tests of the two hypotheses

2.1 Study 1: Are bonobos prosocial toward strangers in the contexts of food sharing and instrumental helping?[1]

2.1.1 Introduction

One of the most puzzling human behaviors from an evolutionary perspective is our species' propensity to share with non-relatives and even strangers (Fehr & FIschbacher 2003, Seabright 2004). Across numerous cultures and early in development, humans engage in spontaneous helping and costly sharing with strangers (Henrich et al. 2005, Warneken et al. 2007). Some have suggested this human form of sharing is inconsistent with the predictions of kinship theory and reciprocal altruism (see Fehr & Fischbacher 2003, but see Delton et al. 2011) while others have proposed our species has evolved unique motivation and cognition for sharing (Tomasello 2009, Burkart et al. 2009, Hill et al. 2009, Silk et al. 2011).

Nonhuman primates are known to help and voluntarily share food with other groupmates (e.g. Stevens 2004, de Waal 1997, Hare & Kwetuenda 2010, Cheney 2011, Feistner & McGrew 1989, Stevens & Gilby 2004). This prosociality, or voluntary behavior that benefits others (Eisenberg et al. 2006, Cronin 2012, Jaeggi et al. 2010, House et al. 2012, Vaish & Warneken 2011), can be driven by selfish or other-regarding motivations (Eisenberg et al. 2006, Fehr et al. 2008). Therefore, while a primate can be prosocial even

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[1] Reprinted from PLoS ONE, 8(1): e51922, Tan, J & Hare, B, 2013, Bonobos share with strangers, under Creative Commons Attribution License (http://www.plosone.org/static/license;jsessionid=B3710233547C96F1E8CE5018429405CA)

if pursuing selfish goals, they only demonstrate other-regarding forms of prosociality if their actions do not result in immediate selfish benefit. A number of experiments have now shown that a variety of primates will even help another individual obtain food when there is no immediate, tangible reward for their help (chimpanzees: Warneken et al. 2007, Melis et al. 2011, Greenberg et al. 2010, Horner et al. 2011, Yamamoto et al. 2009, 2012; old world monkeys: Massen et al. 2010; new world monkeys: Burkart et al. 2007, Lakshminarayanan & Santos 2008, de Waal et al. 2008). This type of prosociality suggests in some contexts primates also have other-regarding motivations (but see critique of this interpretation by Silk & House 2011). However, there remains little evidence that nonhuman primates show any form of prosociality toward non-group members (Burkart et al. 2009, Silk & House 2011, Cheney 2011, de Waal et al. 13, Melis & Semmann 2010). Primates typically compete against non-group members, resulting in agonistic intergroup relations (Crofoot & Wrangham 2010). This hostility goes to the extreme in chimpanzees that opportunistically kill neighbors (Wrangham 1999, Muller & Mitani 2005) and sometimes even immigrants (Kahlenberg et al. 2008, Pusey et al. 2008, Townsend et al. 2007). Therefore, it is unlikely that most primates have tolerance levels that would allow for prosocial or other-regarding tendencies toward strangers. Moreover, designing such an experiment for most primate species would be extremely difficult given the high potential for stress, injury and aggression.

Bonobos are known for relatively high-levels of tolerance within and between groups when compared to chimpanzees (Wrangham 1999, Furuichi 2011, Idani 1991, Hohmann 2001, Wobber et al. 2010a, Hare et al. 2012). In the wild, bonobos have even been observed to have affiliative intergroup interactions. For example, females from neighboring communities have been seen traveling together for days, feeding in the same trees and even participating in socio-sexual behavior (Furuichi 2011, Idani 1991, also see Gold 2001). In a preliminary experiment seven bonobos were given the opportunity to voluntarily share with another bonobo (Hare & Kwetuenda 2010). All three bonobos paired with a non-groupmate voluntarily shared their food while only one of the four bonobos paired with an in-group member shared. No aggression of any form was ever observed. This suggests that with the relative tolerance of bonobos they can afford such prosociality with strangers. In turn, sharing with a stranger might aid them in extending their social network and in forming new "friendships" (Delton et al. 2011, Noë & Hammerstein 1994). However, it remains unclear whether the observed prosociality represents a preference to share with strangers over groupmates. In addition, it is unclear if the voluntary sharing observed only represents a selfish tactic to obtain a novel social interaction or whether bonobos will also share with strangers if there is no immediate, tangible reward. Therefore, we conducted four experiments with 15 wild-born bonobos that are orphans of the bushmeat trade living at Lola Ya Bonobo Sanctuary in Kinshasa, Democratic Republic of Congo (André et al. 2008). We designed

these experiments based on the relative costs and benefits of the prosocial behavior to the actor and this serial design allowed us to identify whether the prosocial motivation is selfish or other-regarding (Table 2). In experiment 1 and 2 we presented bonobos with a task in which they could choose whether to share food and physically interact with either a groupmate or stranger. In experiment 3 and 4 we presented bonobos with a second task in which they could either ignore or help another bonobo in obtaining out-of-reach food. In this second task helping allowed no immediate benefit to the actor (e.g. physical interactions) and the cost of helping was altered between experiment 3 and 4 (see Table 2).

Table 2 Summary of bonobo prosociality in Study 1

		Cost to the actor (food loss and/or energetic cost)	
		High	Low
Potential immediate benefit to the actor (a desirable physical interaction)	Yes	Stranger -Yes[1] Groupmate - No	Stranger - Yes[2] Groupmate - Yes
	No	Stranger - No[4] Groupmate - No	Stranger - Yes[3] Groupmate - Yes

1. Prosociality driven by selfish motivation (i.e. self-regarding preferences): experiment 1-2 of current study; Hare & Kwetuenda 2010; Bullinger et al. 2012 replicated the groupmate results.

2. Prosociality driven by selfish motivation (i.e. self-regarding preferences): The current series of experiments does not examine this type of prosociality since it does not require sharing. Given the results of experiment 1-2, this low-cost, high-benefit context does not allow us to examine the presence of any unselfish motivation. In a setup similar to experiment 1-2, Bullinger et al. 2012 showed that when there was no food to share bonobos in a zoo opened a door for a groupmate, although they also opened the same door at similar rates in a non-social control (i.e. this suggests for groupmates, opening is probably not driven by social reward). We predict in the same contexts bonobos would open the door more frequently for a stranger than in a nonsocial control or for a groupmate since they do this in the current study when it results in the loss of food.

3. Prosociality driven by unselfish motivation (i.e. other-regarding preferences): experiment 3 of current study.

4. Prosociality driven by (stronger) unselfish motivation: experiment 4 of current study; Jaeggi et al. 2010 also confirmed the groupmate results.

2.1.2 Experiment 1

The purpose of experiment 1 was to determine whether bonobos share and prefer to share food with strangers based on Hare and Kwetuenda (2010). The subjects entered a room baited with a pile of highly desirable food. They could either eat all the food alone or they could co-feed with a conspecific by removing a one-way key to

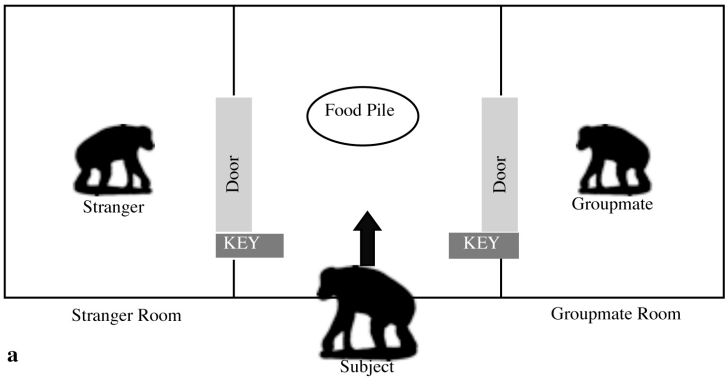
release either a groupmate or a stranger who were each locked in separate adjacent rooms (Figure 2.1.1a).

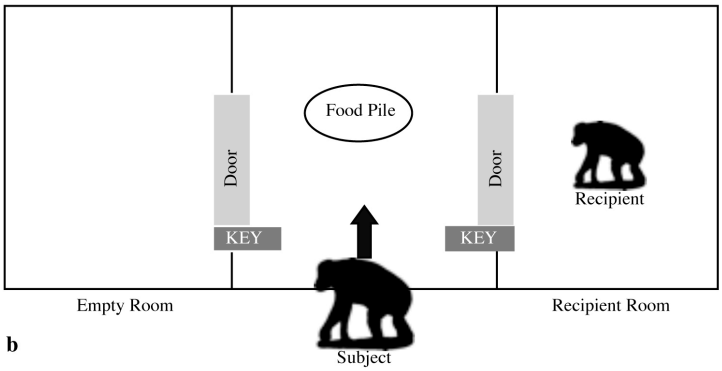
Subjects

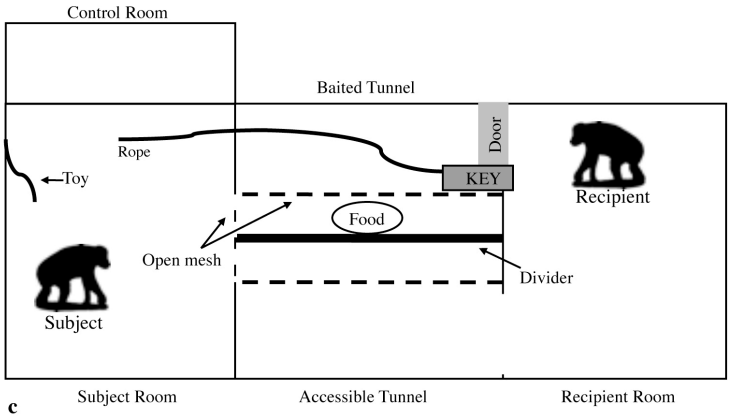
Fourteen bonobos (8F:6M) from Lola ya Bonobo sanctuary participated in this experiment. All experiments were approved by the Ministry of Research in the Democratic Republic of the Congo (#MIN.RS/SG/004/ 2009), Lola ya Bonobo sanctuary and Duke IACUC. All subjects are orphans of bushmeat trade, but a comparison of their psychological health to mother-reared individuals revealed no substantial differences (Wobber & Hare 2011). Each subject was tested with two conspecific recipients – one a stranger and the other a current groupmate. Seven female subjects played the role of the recipient (see Appendix A for pairings). We did not use male recipients simply because we did not have enough available at the time of the experiment. The composition of all trios allowed no role-reversal and maximized combinations of available recipients. Additionally, because pre-existing relationships among groupmates might be a confounding factor, we included as many individuals into the recipient pool as possible and randomly paired each subject with a groupmate recipient.

Strangers were defined as unrelated individuals living in different social groups from one another. All subjects came from two different groups (see Appendix A). Each group has a separate outdoor enclosure and set of indoor sleeping rooms. Strangers

therefore did not have physical access to one another, because they were always physically separated by mesh and an electric fence. There was only possibility for vocal and visual communication, and this resembled the way wild bonobos from different populations interact (Furuichi 2011). Nine of fourteen of our stranger pairings were *complete strangers* who had never stayed in the same physical enclosure prior to the current experiment. We were able to examine individual records at the sanctuary to confirm which subjects were complete strangers. We tested the maximum number of complete strangers we could produce given sample size limitations and management constraints. Two pairings were not complete strangers because they met briefly during testing before they themselves were tested (i.e. they had served as recipients opposite one another for two previously tested subjects). For the last three pairings, they were former groupmates but had been transferred to different groups for at least one year (i.e. a period of time that in captive chimpanzees (*Pan troglodytes*) typically leads to a strong xenophobic response during reintegration attempts, Seres et al. 2001).







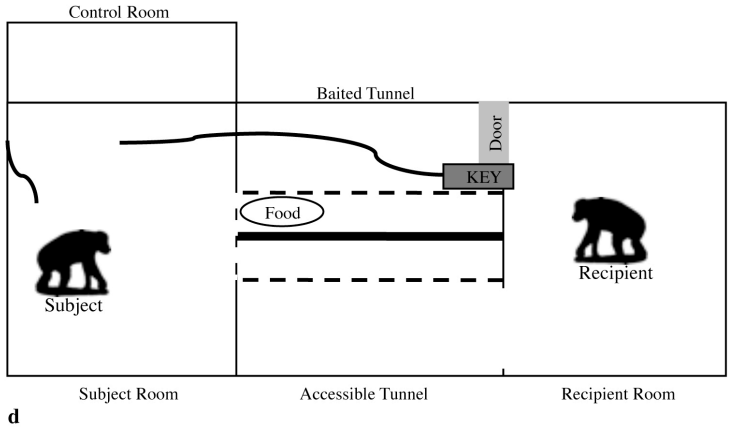


Figure 2.1.1. Setups of experiment 1-4 (a-d)

Setup

The experiment was conducted in three adjacent testing rooms (Figure 2.1.1a). These rooms (each 15m^2) were in the subjects' night building and were separated by open mesh. Manual sliding doors connected the middle room and the two side rooms where the recipients were placed for testing. The middle room also had a separate entrance (i.e. an overhead raceway) through which the subject could enter at the beginning of each test trial. A one-way key system was installed in each of the doors from the middle room into each of the side rooms. The keys consisted of wooden pegs that could be inserted on the subject's side of the door into a round metal hole in the track of the door. This blocked the path of the door unless the key was removed by the subject. Removing both keys simultaneously was impossible due to the distance between them. We thus created a setup in which bonobos in the middle room could determine whether to unlock a door(s) and which door to unlock first.

Procedure

Food introduction: This was designed to demonstrate that subjects understood the one-way key system. One side room was baited with slices of apples or bananas and locked with the one-way key. Subjects had to successfully retrieve food out of the adjacent room in four out of five consecutive trials within 60 seconds.

No-food introduction. This was designed to demonstrate that subjects' door-opening was not simply intrinsically motivating but instead goal-directed. The setup was identical to the food introduction except food was placed in the middle room instead of in one of the side rooms. Subjects needed to inhibit removing the key for 60s in four out of five consecutive trials in less than 21 trials.

Number pre-test. This was designed to demonstrate that subjects could make a choice between the contents of the two side rooms. Both side rooms were locked and one was baited with more food than the other. The locations of food were counterbalanced within and across subjects. Subjects had to first unlock the room with more food in four 1-minute trials of a five-trial session.

Test. For the test a potential recipient was moved into each of the two side rooms – one being a stranger to the subject (as well as the second recipient) and the other being a groupmate of the subject (see Figure 2.1.1a). The location of the different recipients were switched between trials and counterbalanced within and across subjects. Following Hare and Kwetuenda (2010), a mixture of food was placed in a small pile in the center of the food room (i.e. the middle room) beyond the reach of the recipients. A trial started when the subject entered the food room and ended when all the desirable food was claimed or seven minutes after the entry of the subject. Subjects were tested in a five-trial session with the same two recipients throughout, and they were tested early in the morning before their first meal to maximize their food motivation.

Coding and analysis

Based on Stevens and Gilby (2004) and Jaeggi and van Schaik (2011), we define sharing as joint use of monopolizable food. Sharing is a type of prosocial behavior if it is voluntary, i.e. the possessor has the intention to allow the recipient access to food. However, this intention is not necessarily other-regarding or altruistic (i.e. instead they intentionally give another bonobo access to food without concern for the recipient's well-being).

As the measurement of sharing, door-opening was coded when a subject *first* removed the key to one of the doors but *only* if this occurred before all desirable food was *claimed*. Following Hare and Kwetuenda (2010), food being "claimed" was scored when a bonobo (both subjects and recipients) picked up each of the different pieces of food. This conservative criterion means only food that subjects did not pick up in the original food pile before releasing one of the recipients was scored as potentially sharable (i.e. food that subjects claimed but dropped might not represent their intention to share and would be excluded). Because a trial could take up to seven minutes, it was also possible for the second door to be opened releasing the second recipient before the end of the trial. A second door-opening was scored when either the subject or the first recipient removed the key to the second door - again only if this occurred before all the desirable food was claimed.

We coded food consumption if an individual placed food into its mouth. Because the bonobos could take a handful of food at once, we were unable to track the exact amount of food each recipient consumed. As a proxy, we compared "shared" feeding-time (i.e. from when a recipient was released until when all food was consumed) to total feeding-time (i.e. from when the subject started feeding to when all food was consumed). Socio-sexual behavior was scored when genital-genital contact occurred between two individuals once a recipient door was opened and before all the desirable food was claimed. Similarly, aggression was also scored if one bonobo fought with another bonobo resulting in screaming, hitting and biting. To assess the effect of recipients' solicitation, we categorized the recipient in each trial as either 1) *active* if they made any attempt to open the locked door or to reach the food, or 2) *passive* if no such behavior was observed. Inter-coder reliability was high (door-opening, food consumption, socio-sexual behavior, aggression: Cohen's $\kappa = 1$; signaling behavior: $\kappa = 0.720$; feeding time: $N = 12$, $r = 0.993$, Spearman's correlation). Nonparametric, two-tailed statistics were used in all analyses.

Results

See Figure 2.1.2a for results for a sample video. The majority of the subjects (12 of 14) shared at least once and for a total of 51 trials (out of 70, or 72.9%). Subjects chose to release a complete stranger in preference to a groupmate before eating all the food ($N = 9$

(two ties), Z = 1.961, p = 0.05, Wilcoxon test), while having a strong tendency when all strangers are included (N = 14 (two ties), Z = 1.737, p = 0.081, Wilcoxon test). Nine subjects released the stranger first in more trials than the groupmate and only three subjects were in the opposite direction (see Appendix A). Subjects also allowed the stranger but not the groupmate to co-feed for the majority of the total feeding time (stranger: N = 10, T = -2.090, p = 0.037; groupmate: N = 6, T = -0.105, p = 0.917, one-sample Wilcoxon signed rank test). Moreover, while unexpected, the second recipient was often released after the first even though there was remaining food that would need to be shared three ways. When the subject released the stranger first, the second recipient (the groupmate) was released by this first recipient (the stranger) more often than by the subject (N = 8 (one tie), Z = 1.983, p = 0.047, Wilcoxon test, Figure 2.1.2a).

Subjects consumed part of the food before releasing a recipient in 86.3% of trials where sharing occurred (44 of 51). The released recipients obtained desirable food in 78% of the trials (40 of 51). No form of aggression was ever observed. Socio-sexual behavior between the subjects and the first recipient released was observed in 20 trials (39.2%). This behavior only occurred between strangers but not groupmates (N = 51, r = 0.494, p < 0.001, Phi coefficient). We found no co-variation between socio-sexual behavior and consumption of food by the recipient within trials where subjects unlocked a door (N = 51, r = 0.128, p = 0.360, Phi coefficient). Recipients' signaling behavior also did not correlate with subjects' tendency to share (N = 60, r = 0.074, p = 0.573, Spearman's

correlation). Finally, subjects' prosociality did not change between the first and the last two trials (tendency to release a recipient: N = 14, Z = -0.378, p = 0.705; preference for releasing the stranger: N = 14, Z = -0.427, p = 0.669, Wilcoxon test).

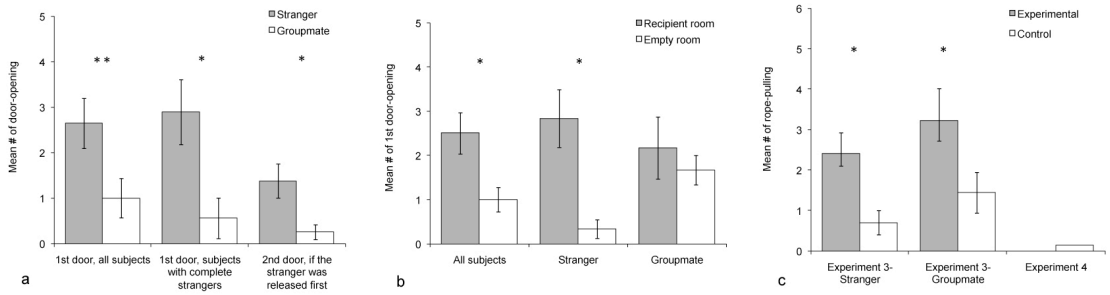


Figure 2.1.2 Results of experiment 1-4. ** p ≤ 0.10, * p ≤ 0.05

Discussion

Our results show that bonobos voluntarily share food with a recipient even when they could have monopolized it. They preferred to release the stranger and they allowed the stranger but not the groupmate to co-feed for the majority of total feeding time. Also, the surprising finding that the strange recipients voluntarily allowed a second recipient that was also strange to them into the same room (i.e. letting themselves be outnumbered by strangers) contrasts sharply with the xenophobic response of wild chimpanzees (i.e. wild chimpanzees rapidly retreat if they do not outnumber strangers by a factor of three; see Wilson et al. 2001).

The subject's door opening was not a result of an inability to inhibit opening the door or inhibit interacting with the recipient. First, door-opening itself was not intrinsically motivating because in the no-food introduction subjects did not remove the key when there was no incentive to do so. Second, a preference for a specific recipient type is not predicted if door-opening alone motivated their choices. Third, bonobos are as capable of inhibiting door-opening as chimpanzees and 4-5-year-old children if it leads to food loss (Vlamings et al. 2010). Fourth, Hare and Kwetuenda (2010) previously demonstrated that some of these same bonobos tested again here do not open a door while eating food in the test room when other attractive items are in one of the adjacent rooms (i.e. additional food). Therefore, the subject's behavior was a voluntary choice to release the recipient over immediate feeding. As a result they intentionally forfeited some of the monopolizable food to the recipient (regardless of whether this sharing was selfishly or unselfishly motivated).

Subjects all passed the pretests and showed no temporal change in door-opening, which suggests that they clearly understood the consequence of opening the door. Subjects also did not open the door and then simply monopolize all the food. After being released by the subject, recipients consumed food in the majority of the trials (78%). Subjects were also highly food motivated since in 86.3% of trials they ate some food before sharing. In addition, we used an amount of desirable food that we knew subjects eat in its entirety based on a previous non-social control test (see Hare & Kwetuenda

2010; we facilitated this by testing subjects before their morning meals). Subjects' door opening cannot be explained by tolerated theft or sharing-under-pressure, because the subjects had complete control over the food. No physical harassment was possible and no aggression was ever observed. The signaling behavior of the recipients also did not influence the subjects' sharing preference.

Reciprocal altruism is also not a plausible explanation for these results. First, there were no role reversal between subjects and recipients. This eliminates the possibility for tit-for-tat within the experiment. Second, reciprocal exchange before or after the testing period was impossible between non-groupmates. Third, contingent interchange of food-for-reproductive sex is not supported. Intercourse between a tumescent female and male was never observed. Non-reproductive socio-sexual behavior occurred at a low rate (39.2% of sharing trials). All of this occurred between female-female dyads or males and detumescent, pre-pubertal juveniles. Although socio-sexual behavior only occurred between stranger pairs, it did not correlate with food consumption by the recipient. Therefore, socio-sexual behavior was likely a by-product of sharing instead of the motivation behind the sharing behavior (also see Woods & Hare 2011).

Experiment 1 replicated the findings of Hare and Kwetuenda (2010) that bonobos voluntarily chose to share monopolizable but highly desirable food with one another, including strangers. It further confirmed that bonobos have a xenophilic preference

toward strangers over groupmates when sharing food. However, it was unclear whether this was caused by an inclination to share with strangers and/or a tendency to avoid groupmates. We adopted a between-subject design in experiment 2 to address this question.

2.1.3 Experiment 2

In experiment 2, only one recipient was placed in one of the two adjacent rooms leaving the second adjacent room empty (see Figure 2.1.1b). For half of the subjects the potential recipient was a groupmate while for the other half she was a stranger. If the subjects were motivated to share, they should unlock the recipient room more often than the empty room.

Methods

Because the current experiment examined the preference of door-opening instead of its occurrence, we tested all twelve bonobos (8F:4M) that participated in experiment 1 that opened a door in at least one trial (see Appendix A). Six subjects were paired with a groupmate and six with a stranger (five with a complete stranger). The location of the recipient was counterbalanced within subject.

The setup of experiment 2 was identical to experiment 1 with the exceptions that only one recipient was placed in one of the side rooms (leaving the other side room empty) and no pretests were conducted since this experiment was conducted days after

the completion of experiment 1. In addition, having the empty room in this experiment served as an internal, non-social control for the intrinsic value of opening doors (Hare & Kwetuenda 2010).

Strangers and behaviors were defined as in experiment 1. Nonparametric tests were applied throughout. Given the results of experiment 1 and of Hare and Kwetuenda (2010) showing prosocial sharing and a preference to share with strangers in bonobos, one-tailed statistics were used in comparing 1) rates of opening the recipient's door and the empty room and 2) rates of releasing the recipients between the two groups of subjects. All other analyses were two-tailed. Our primary measures followed those in experiment 1. Inter-coder agreement was high (feeding-time: $N = 9$, $r = 0.987$, Spearman's correlation; all other measures, Cohen's $\kappa = 1$).

Results

The majority of the subjects (11 of 12) unlocked the recipient at least once and for a total of 30 trials (out of 60 or 50%). Overall, the subjects unlocked the recipient door first more often than the empty room ($N = 12$ (two ties), $Z = 1.955$, $p = 0.026$, Wilcoxon test, one-tailed, Figure 2.1.2b). However, subjects only first opened the recipient's door more than the empty door when the recipient was a stranger (groupmate: $N = 6$ (one tie), $Z = 0.552$, $p = 0.291$; stranger: $N = 6$ (one tie), $Z = 2.023$, $p = 0.022$; complete stranger: $N = 5$ (one tie), $Z = 1.890$, $p = 0.030$, Wilcoxon test, all one-tailed, Figure 2.1.2b). When

comparing the difference score between the rates of opening each door, subjects paired with a stranger again showed a stronger preference for unlocking the recipient door than those paired with a groupmate (all strangers: N =12, U = 5.5, p = 0.021; pairs of complete strangers: N =11, U = 5.5, p = 0.041, Mann-Whitney test, all one-tailed). Consistent with experiment 1, subjects again released strangers such that they could eat for the majority of the total feeding time, but here they also did the same for their groupmate (stranger: N = 6, T = -2.207, p = 0.014; groupmate: N = 5, T = -2.023, p = 0.022, one-sample Wilcoxon signed rank test). Subjects consumed some of the food before sharing in 76.7% (23 of 30) of trials. Recipients were able to eat food in the 80% of trials once released. Socio-sexual behavior was only observed in nine trials (of 30 sharing trials) in four stranger pairings and one groupmate pairing. It only occurred between female-female dyads and male-juvenile-female dyads. Again subjects' tendency to share neither correlated with recipient's request (N = 60, r = 0.052, p = 0.694, Spearman's correlation, two-tailed) nor changed between the first two and the last two trials (N = 12 (six ties), Z = -0.816, p = 0.414, Wilcoxon test, two-tailed).

Discussion

The results of experiment 2 further support the idea that sharing was voluntary, prosocial and xenophilic. Subjects made a clear choice to share monopolizable food with strangers, while they were indifferent regarding groupmates (i.e. they did not avoid or

approach groupmates). We thus confirmed that the results in experiment 1 were driven by an inclination to share with strangers.

Again subjects' behavior suggests door-opening was not simply caused by a lack of inhibitory control, because subjects opened doors according to the identity of the recipient not just the presence of a conspecific. Subjects were also food motivated since they ate in 76.7% of trials prior to sharing. Despotism cannot explain the results since the released recipients indeed ate food 80% of time. Interchange of food-for-sex is again not supported. Socio-sexual behavior occurred at a low frequency (30%) and had no reproductive function.

The results of the first two experiments show that bonobos are prosocial toward strangers, because the observed sharing was both voluntary and beneficial to others (Eisenberg et al. 2006). Subjects intentionally provided the recipient access to food by opening the door. They did this repeatedly across trials even though in other nonsocial contexts they quickly learn to avoid choices that lead to the loss of much smaller amounts of food (Vlamings et al. 2010, Rosati & Hare 2012). However, this willingness to relinquish food to others could be driven by two possible motivations (see Table 2). First, bonobos may only share food to facilitate a physical interaction with a stranger. Essentially, this type of food sharing is analogous to a form of tool-use where food sharing selfishly functions as a way to access a stranger. This predicts that the reward of initiating a novel interaction is so high that bonobos are willing to give up desirable food

in exchange. However, if this alone motivates bonobos sharing they will not share when a physical interaction is impossible. Second, the observed sharing may in part be driven by other-regarding preference, an unselfish motivation based on concerns with other's welfare. This possibility is suggested by the fact that the food-motivated subjects could have easily monopolized all the food before releasing a recipient to interact. Instead, they chose to share. This motivational hypothesis predicts that bonobos will continue sharing with others even in contexts where a physical interaction is not possible. To test for the relative contribution of these motivational explanations, we designed a helping task in experiment 3 and 4 that allowed no physical interaction between participants. As a result, there was no immediate benefit for behaving prosocially, while the cost of helping was altered between experiment 3 and 4 (Table 2).

2.1.4 Experiment 3

The purpose of experiment 3 was to determine whether bonobos are prosocial to strangers even if there is no immediate, tangible benefit. Subjects could pull a rope to release a recipient (a stranger or a groupmate) to acquire out-of-reach food. To raise the cost of the prosocial act, a novel toy was placed in the subjects' room so that helping also required forfeiting time playing. Importantly, the subject and the recipient were always physically separated, and the subject had no way to bring the recipient any closer (see Figure 2.1.1c).

Subject

Ten bonobos (5F:5M) participated in this experiment (see Appendix B). Subjects were chosen based on their spontaneous level of comfort in the current experimental set-up (i.e. not all subjects were comfortable playing in the tunnels). All except one (Chibombo) had been tested in experiment 1 and 2 over a year before the start of this experiment. All except Sake were separately tested with both a stranger and a groupmate recipient. We were only able to pair Sake with a stranger due to time and space limitations. Of all 10 subject-stranger pairs, 7 were complete strangers. Recipients could be either female or male, but the stranger and the groupmate of any one subject were sex-matched. As in the previous two experiments no reciprocity could occur between the subject and the recipient based on how recipients were assigned.

Setup

The experiment was conducted in the subject room and the recipient room that were connected by two parallel tunnels (see Figure 2.1.1c). In addition, a control room (i.e. an overhead raceway) was adjacent to the subject room. In both tunnels the door to the recipient room could be locked with a one-way key installed inside the tunnel. The key was attached to a rope extending into the subject's room allowing subjects to potentially unlock the door. A divider was installed between the tunnels. A bonobo in one tunnel could reach through the tunnel mesh into the space between the divider and

the tunnel, but they could not reach through the divider into the other tunnel area. This prevented recipients from obtaining food placed next to one tunnel from the opposite tunnel .

Procedure

Self-regard pre-test. This was designed to test whether subjects understood the physical set-up of the task. In this pre-test, subjects had to open one of the tunnels so they themselves could access the out-of-reach food (i.e. showing self-regard). The doors to both ends of one tunnel (the accessible tunnel) were open, which allowed the subject to travel between the two rooms. The other tunnel was baited with food and locked by the one-way key. Two slices of banana were placed in the space between this tunnel and the divider, and they were thus inaccessible from either the subject or the recipient room. The tunnel in which the food was placed was counterbalanced between trials. In order to enter the baited tunnel to retrieve the food, the subject had to pull the rope in the subject room and then travel through the accessible tunnel to open the door in the recipient room. Once the subject solved this problem on five consecutive trials within 60 seconds, they could proceed to the next pre-test.

No-food introduction. This session was designed to demonstrate that subjects did not simply find key removal intrinsically motivating. The configuration of the baited tunnel remained the same as the self-regard pre-test with the major exception that

subjects had no possibility of retrieving the food (i.e. five banana pieces). As before, the door from the accessible tunnel into the recipient room was left open; whereas the door from this same tunnel and the subject room remained locked (such that removing the key blocking the door between the food tunnel and the room opposite to the subject room would not help subjects in obtaining the food). In addition, an attractive novel toy (a rope with a PVC tube attached) was placed in the subject room to provide an alternative activity to helping (based on Warneken et al. 2007, Melis et al. 2011). Finally, no other bonobos were present in any room adjacent to the subject room during this test. To proceed to the test on each of the two testing days (see below), subjects needed to inhibit pulling the rope for 60s in five consecutive trials.

Test. Subjects were tested with the two different recipients on a separate day. The order of this testing was counterbalanced across subjects. For each recipient subjects were first tested in the no-food introduction and then received six experimental trials and six control trials in a block design. The order conditions were administered was counterbalanced across subjects. This means subjects received 12 test trials on each day or a total of 24 test trials. This design was used when the subject was tested with both the groupmate and the stranger. The order in which the stranger or groupmate recipient was paired with the subject was counterbalanced between subjects.

As seen in Figure 2.1.1c, the procedure of these trials were identical to the non-food introduction with the exception that in the experimental condition another bonobo

was present in the recipient room and during the control condition the same recipient was in a room adjacent to the subject (the control room). As a result the subjects and the recipient were always physically separated. It is also important to note that pulling in the experimental condition could never bring the recipient in closer proximity, because it could always enter the accessible tunnel. Therefore, helping could not be motivated by the potential for a physical social interaction. In addition, a recipient was always present in a room adjacent to the subject room in both conditions. Therefore, unlocking the tunnel could not be explained by social facilitation (i.e. this followed the design of Melis et al. 2010, Warneken et al. 2007).

Coding and analysis

Our main measure was rope-pulling. We scored a *rope-pull* when subjects pulled the rope attached to the key causing the key to be removed from the door within 60s. We also coded a number of other behaviors to assess whether subjects' rope-pulls were somehow contingent on the behavior of the recipient. To assess the possibility of local enhancement caused by the recipient's positioning behavior, we coded how often a recipient was directly behind the locked door to the baited tunnel while the subject was looking on from behind their door to the same tunnel. Although the subject and the recipient were always separated by mesh, we scored social contact if there was any affiliative behavior (hugging, grooming, tickling and touching genitals) between the

mesh. Signaling behavior was coded based on the same definition used in experiment 1 and 2. Inter-coder agreement was high (rope-pull: $\kappa = 0.906$; local enhancement: $\kappa = 0.781$; social contact: $\kappa = 0.841$; signaling: $\kappa = 0.933$). All statistics were nonparametric. Based on the prosociality observed in experiment 1 and 2, directional predictions were made and one-tailed statistics were used to compare 1) between the experimental and control conditions, 2) between subject's behavior with stranger and groupmate recipients. All other statistics were two-tailed.

Results

The majority of the subjects (9 of 10) helped the recipient at least once. Subjects pulled the rope in the experimental condition more often than in the control for both the stranger and the groupmate (stranger: pulling rate in the experimental condition = 40±8.7%, in the control condition = 11.7±5%, $N = 10$ (two ties), $Z = -2.263$, $p = 0.012$; groupmate: pulling rate in the experimental condition = 53.7±13.3%, in the control condition = 24±8.4%, $N = 9$ (one tie), $Z = -2.257$, $p = 0.012$, Wilcoxon test, all one-tailed, Figure 2.1.2c). They also helped the two categories of recipients equally often ($N = 9$ (four ties), $Z = -0.137$, $p = 0.446$, Wilcoxon test, one-tailed). The subjects' other-regarding preference did not vary with the sex of the recipient (stranger: $N = 10$, $U = 5.5$, $p = 0.136$; groupmate: $N = 9$, $U = 8.5$, $p = 0.151$, Mann-Whitney U test, two-tailed). However, the subjects' other-regarding preference was more xenophilic when the recipients were

female than male (N = 9, U = 1.5, p = 0.029, Mann-Whitney U test, two-tailed, see Appendix B). Male and female subjects did not differ in their tendency to help a recipient (stranger: N = 10, U = 10.5, p = 0.690; groupmate: N = 9, U = 6, p = 0.413, Mann-Whitney test, two-tailed) or their preference for helping a specific recipient (N = 9, U = 5.5, p = 0.247, Mann-Whitney test, two-tailed, Appendix B).

The subjects' tendency to pull did not change between the first and the second half of a 12-trial session in one testing day (N = 10 (five ties), Z = -0.816, p = 0.414, Wilcoxon test, two-tailed), or when comparing their pulling rates between the first and the second recipient with which they were paired (i.e. between two testing days, N = 9 (four ties), Z = -0.412, p = 0.680, Wilcoxon test, two-tailed). The subjects' likelihood of pulling was not related to whether the recipient was directly behind the locked door or not (N = 8 (one tie), Z = -0.25, p = 0.799, Wilcoxon test, two-tailed). Helping did not increase the subjects' chances of having between-mesh social contact with the recipient (N = 9 (one tie), Z = -1.402, p = 0.161, Wilcoxon test, two-tailed). In addition, they were less likely to respond to an active than a passive recipient (chances of helping an active recipient: 41.86±12.25%; a passive recipient: 80.56±16.34%, N = 6 (one tie), Z = -2.023, p = 0.043, Wilcoxon test, two-tailed).

Discussion

These findings show that even when there was no immediate social reward,

bonobos are still motivated to help a stranger acquire out-of-reach food. Unlike experiment 1 and 2, not only strangers but also groupmates can become recipients of this prosocial act. Moreover, this prosociality could be directed to both male and female recipients, although subjects were more xenophilic toward females. These results do not support the hypotheses that other-regarding preference toward strangers is completely unique to humans (Fehr & Fischbacher 2003, Burkart et al. 2009, Silk & House 2011, Cheney 2011). The sharing behavior of bonobos at least in part seems to be motivated by other-regarding preferences in addition to the desire to physically interact with strangers. Several low-level alternatives can be ruled out. Subjects all passed the self-regard pre-test, demonstrating clear understanding of the physical setup. They were always separated from the recipient and were not harassed into helping. Learning is also an implausible explanation. First, subjects' behavior did not change over time in the test. Second, all subjects passed the no-food introduction (i.e. no pulling for five consecutive trials). To make sure that they clearly understood that the food could not be obtained, we conducted the experimental and control sessions immediately after this no-food introduction. Therefore, it is unlikely subjects were removing the key in the experimental and control sessions because they were trying to acquire the food for themselves.

Local enhancement (i.e. the proximity of the recipient to the food or keys) cannot explain the observed helping since it had no effect on the subjects' likelihood of rope-

pulling. It is also unlikely that the subjects' rope-pulling was motivated by a desire to bring the recipient into closer proximity, because 1) unlocking the baited tunnel did not bring the recipient into closer contact with the recipient since the other tunnel already allowed the recipient to potentially approach the subject (Figure 2.1.1c), and 2) experiment 1 and 2 predict more helping of strangers than the groupmates if increasing proximity was the subjects' sole motivation for helping. In addition, releasing the recipient did not increase rates of social contact. Reciprocity is again unlikely since role-reversals did not occur during the test and no repayment before or after the test was possible between strangers.

Experiment 3 shows that bonobos are motivated to help strangers even when the prosocial act has no immediate benefit (i.e. a physical interaction) but incurs a cost (see Table 2). In experiment 4, we test whether subjects will continue to help when there is no immediate benefit and an even greater cost to helping (loss of one's food).

2.1.5 Experiment 4

In this final experiment the same paradigm from experiment 3 was used with the exception that food was placed within the subject's reach so that if the recipient was released both individuals had equal access to the food (Figure 2.1.1d). Helping would require subjects to forfeit food in their possession and did not create an opportunity for physical interaction since the subject and recipient still remained in separate rooms.

Methods

Seven bonobos (4F:3M) participated in this experiment. All were subjects from experiment 3. Four were paired with a stranger and three with a groupmate (Appendix B). The experimental design was identical to experiment 3 with the major exception that the baited food was moved within reach of the subject (see Figure 2.1.1d). Subjects could easily reach through their door into the tunnel and eat the food or they could choose to release the recipient and eat the food together. All behavioral measures were the same as those used in experiment 3. Cohen's κ of the recipient's behavior was 0.895.

Results and discussion

No subject ever released a recipient in an experimental trial. A single subject opened the door in one control trial. The refusal to release the recipient was not due to a loss of skill at opening the doors since subjects again passed a pre-test and again showed self-regard before the experiment began. This lack of helping also was not in response to a decrease in the recipient's requesting behavior, since it did not differ between experiment 3 and 4 (the recipient's chances of requesting in experiment 3: 89.29±6.98%; experiment 4: 69.05±8.47%, $N = 7$ (no tie), $Z = -1.439$, $p = 0.15$, Wilcoxon test, two-tailed). Instead the same subjects who helped in experiment 3 refused to share in experiment 4.

Although prosociality in experiment 1-2 and experiment 4 both incurred a high cost of food loss, sharing did not occur when subjects had no access to the recipient. This

suggests that the xenophilic sharing observed in experiment 1-2 was in part motivated by a desire to initiate a physical interaction with the stranger (with potential for full body contact), and the payoff of this interaction was so high that they were even willing to forfeit highly desirable food to facilitate it (see Table 2). In experiment 4 there was so little opportunity for physical interaction that the benefit of the interaction no longer outweighed the cost in food (i.e. subjects could only potentially reach hands and feet through the bars to touch). As a result, subjects no longer shared with groupmates or strangers.

2.1.6 General discussion

Our results demonstrate that prosociality and even other-regarding preferences toward strangers are not unique to humans. Our results also raise the possibility that bonobos have a unique prosocial preference for strangers over groupmates (i.e. while humans share with strangers they do not prefer them over groupmates: Fehr et al. 2008, Levine et al. 2005). Our findings highlight two distinct motivations underlying prosociality toward strangers (see Table 2). First is a xenophilic motivation. In experiment 1 and 2 bonobos are willing to forego food in their possession to facilitate an interaction with a stranger – even preferring a stranger to a groupmate. However, this type of xenophilic sharing has limits. In experiment 4 bonobos will not give up valuable food in their possession unless a desirable social interaction is possible (see also Jaeggi et al. 2010). This supports the hypothesis that the relatively high tolerance observed in

bonobos allows them to potentially extend their social networks through interactions with strangers (Engh et al. 2006, Taylor et al. 2000). However, bonobo sharing is not completely selfishly motivated either. We also discovered a second, unselfish motivation toward strangers. In experiment 3 bonobos do exhibit other-regarding tendencies when no immediate payoff is available. Bonobos will exert effort to help strangers (and groupmates) obtain out-of-reach food as long as the cost of such helping is relatively low (i.e. does not require giving up food in their possession).

Controls demonstrate that the bonobos understood the physical properties of the two tasks (i.e. by demonstrating self-regard in a non-social pre-test) and were not opening doors due to local enhancement or a lack of inhibitory control. The observed sharing also cannot be explained by social factors including: harassment, since only subjects could allow recipients to approach the food; kinship, since no participant is related; repayment, since no reciprocal exchange before or after the experiment could occur between non-groupmates; and solicitation, since subjects' door opening behavior is not related to the requests of the recipients.

We predict future research with other captive bonobo populations will show a similar tendency for prosociality toward strangers since wild bonobos have the potential to affiliate with neighboring groups (Furuichi 2011) and comparisons between the sanctuary bonobos and other captive bonobo populations have shown similar results in other cognitive domains (Wobber & Hare 2011). Correspondingly, the xenophobia

observed in captive chimpanzees mirrors the lethal aggression they can show toward neighboring groups in the wild (i.e. introducing chimpanzees to a pre-existing group often leads to serious injury and even fatalities; Seres et al. 2001, Brent 2001). It is also unlikely that bonobo's attraction to strangers is an expression of a more general preference for risk and novelty, since bonobos are more risk averse in foraging contexts (Heilbronner et al. 2008) and more neophobic in non-social contexts (Herrmann et al. 2011) than chimpanzees. However, we also predict that future research will likely find variation in xenophilic sharing among bonobos depending on the age and sex combination of the actor and recipient. Throughout our experiments the majority of our subjects were juveniles and young adults (<15 years old; see Appendix C showing age of sexual maturity for sanctuary bonobos is between 7-8 years of age). In addition, the recipients in experiment 1 and 2 were always female. It is likely that older bonobos or even male-male pairings of bonobos will not show the same xenophilic preference observed in experiment 1 and 2. Given the variance observed in social behavior across different populations of wild chimpanzees (Stumpf 2011) it is also possible that some chimpanzee pairings might show a xenophilic preference (i.e. male actors might prefer strange, adult female recipients). If an ethical way to test chimpanzees could be designed it would be interesting to know when and if they ever show a xenophilic preference for sharing with conspecifics (see Herrmann et al. 2011 for evidence of xenophilia towards humans in chimpanzees). Another important future extension of the current work

would be to test whether bonobos are more or less willing to share with groupmates based on their relationship quality during their natural group interactions. It may be that bonobos do readily volunteer to share with specific groupmates even though they do not prefer to share with all groupmates.

The current findings suggest that prosociality and even other-regarding behavior toward strangers is likely constrained across species by intergroup tolerance. Therefore, xenophilic prosociality is present in a species without language, social norms, intergroup violence or cooperative breeding because the benefits of initiating a new "friendship" and therefore expanding individual social network (Noë & Hammerstein 1994, Engh et al. 2006, Taylor et al. 2000, Silk 2007) outweighed the costs of a prosocial interaction with a stranger (e.g. lethal aggression or feeding competition) (Wrangham 1999, Kappeler & van Schaik 2002). With little chance of serious conflict arising from intergroup interactions bonobos can more quickly develop positive relationships with non-group mates than groupmates with whom they have a long history of interactions (i.e. more social effort is needed to improve an existing relationship than to establish a completely new relationship). Future research will be necessary to establish if the relatively pacific bonobo is unusual among nonhumans in this regard or whether other species behave similarly toward strangers (Ganem & Bennett 2004). In addition, it is possible that bonobos may provide costly help to strangers in other contexts (although a method to non-verbally test nonhuman preferences toward an anonymous social partner

remains elusive precisely because anonymity relies on linguistic capabilities).

Our findings suggest that the initial step toward the evolution of prosociality toward strangers may be selection against xenophobia (Ganem & Bennett 2004, Hare 2007, Hare et al. 2012), instead of selection facilitated by xenophobic aggression (Choi & Bowles 2007). As a result, bonobos may be unique among apes in preferring to interact with strangers over groupmates even at the cost of sharing food. For humans, an increase in social tolerance likely resulted in bi-sexual dispersal and an expanded social network of unrelated individuals (Hill et al. 2011), which further enabled cumulative culture and cooperation (Foley & Gamble 2009, Tomasello 2009). Based on current evidence, it is likely that humans are unique for the ability to extend our ape-like prosociality even to the most costly of contexts. These extreme other-regarding preferences possibly rely on language and social norms making it unlikely that such preferences preceded the evolution of these socio-cognitive abilities (Hill et al. 2009).

2.2 Study 2: Are bonobos prosocial toward strangers in the prosocial choice task?[2]

2.2.1 Introduction

[2] Reprinted from manuscript, Tan J, Kewtuenda S, & Hare B, in prep, Do bonobos donate food in a prosocial-choice task?

Prosocial behavior, or voluntary behavior that benefits others (Eisenberg et al. 2006), is a universal human phenomenon observed across cultures and early in development (Henrich et al. 2005, Warneken and Tomasello 2006). Humans are even willing to help, inform or share with others when the actor receives no immediate, tangible rewards (Fehr and Fischbacher 2003, Warneken and Tomasello 2009). This suggests that humans are capable of the type of prosociality that is motivated by unselfish concerns with others' welfare, or other-regarding motivations (Silk et al. 2005). Nonhuman primates are known for some degree of prosociality, even if the underlying motivation may be selfish (de Waal 1997, Stevens 2004, Gilby 2006, Hare and Kwetuenda 2010). However, whether they share other-regarding motivations with humans remains controversial.

Experimental approaches to this problem have yielded mixed results from two major paradigms. The instrumental helping paradigm presents subjects with an opportunity to pay an energetic cost to help a recipient retrieve an out-of-reach item (Warneken and Tomasello 2009). In the experimental condition, helping is both needed because the recipient explicitly expresses the desire for the item, and possible because the experimental setup allows the subjects to help. In the control condition, helping is either unnecessary or ineffectual. Like human infants, both chimpanzees and bonobos demonstrated a higher rate of helping behavior in the experimental than in the control condition (Warneken and Tomasello 2006, Warneken et al. 2007, Yamamoto et al. 2009,

2012, Greenberg et al. 2010, Melis et al. 2011, Tan and Hare 2013, see also positive results in a capuchin helping experiment: Barnes et al. 2008). This helping behavior has been observed even when it is not rewarded, when the out-of-reach item is desirable food, when the recipient is an unfamiliar human, an unrelated conspecific and in the case of bonobos, a stranger from another social group. It is important to note that *before* the subjects are tested for other-regard, a self-regard pretest has always been conducted to show that they have understood the contingency of the apparatus and could utilize it to achieve self-rewarding results. Therefore, these results support that nonhuman apes share other-regarding motivations with humans (de Waal 2008, Hare and Tan 2011, Warneken and Tomasello 2009).

Other researchers adopted a prosocial choice task to address this question. Originally developed by Silk et al. (2005) and Jensen et al. (2006), this paradigm requires the subjects to make a direct choice between a prosocial option, which delivers food reward to both the actor and a recipient in an adjacent room (1/1), and an asocial option, which delivers the same amount of food to the actor but none to the recipient (1/0). Other-regarding motivations are observed if the subjects choose the 1/1 option more frequently in the experimental condition where the recipient is present compared to a recipient-absent control condition. Initial experiments have found that they were indifferent to whether the recipient would receive food (Silk et al. 2005, Jensen et al. 2006, Vonk et al. 2008).

This discrepancy has raised questions regarding the intuitiveness of the prosocial choice experiments with chimpanzees. The first criticism is based on concerns over the study design. In these prosocial choice experiments, the subjects could make a choice by pulling one of two mobile, baited platforms installed in a mechanical trolley system (Silk et al. 2005, Jensen et al. 2006, Vonk et al. 2008). The subjects had not successfully passed a pretest to definitively show self-regard *before* they were tested for other-regard. As a result, it is possible that the subjects did not understand or misunderstood the contingency of the task when they had to utilize it to benefit others (Hare and Tan 2011).

The second explanation hypothesizes that the presence of food, a highly contested resource in chimpanzee societies, constrained their prosociality (Hare 2001, Warneken and Tomasello 2009). When choosing the two options, the chimpanzees are likely (1) pre-occupied with acquiring their own food pieces (Warneken and Tomasello 2006) and/or (2) lacking the natural behavior repertoire to actively transfer desirable food to others (Gilby 2006, Ueno and Matsuzawa 2004). This argument is consistent with several instrumental helping experiments that have found chimpanzees would actually help others acquire food when they are not engaged in acquiring food for themselves (Warneken et al. 2007, Melis et al. 2011). Finally, a recent study with chimpanzees used tokens to indirectly represent the food distribution of 1/1 and 1/0. Although no self-regard pretest was conducted, the authors reported a positive result and argued that the

token approach has successfully lessened the pre-occupation for food (Horner et al. 2011, but see Yamamoto and Tanaka 2009).

Overall chimpanzees seem at best inflexible in the prosocial choice task, even though there is a growing literature that some monkey species show signs of other-regarding motivations in similar situations (macaques: Massen et al. 2010, Chang et al. 2011; capuchins: Lakshminarayanan and Santos 2006, de Waal et al. 2008, Takimoto et al. 2009; callitrichids: Burkart et al. 2007, Cronin et al. 2009, 2010, Stevens 2010). Given the extensive food sharing behavior observed in humans under natural and laboratory situations (Gurven 2005, Brownell et al. 2009, Hamann et al. 2011, Warneken et al. 2011), this might have indicated a crucial difference between human and nonhuman ape prosociality when it comes to food. One of the key shifts during human evolution might be lifting a chimpanzee-like constraint on intense feeding competition and extending other-regards into the domain of sharing food (Warneken and Tomasello 2009). However, it is difficult to come to any conclusions without examining bonobos.

As the other closest living relative of humans, bonobos are thought to experience weakened feeding competition relative to chimpanzees because bonobos live in a richer, gorilla-free habitat (Malenky and Wrangham 1994, Wrangham & Peterson 1996, but see Hohmann et al. 2010). This results in a tendency to avoid social competition in foraging contexts (Wobber et al. 2010a), and a higher co-feeding tolerance allowing bonobos to outperform chimpanzees in collaborative tasks that entail sharing monopolizable food

(Hare et al. 2007, but see Jaeggi et al. 2010a for a very uncommon measure of feeding tolerance). Perhaps the most striking observation is that they would voluntarily release another bonobo to co-feed on a pile of highly desirable food that could have otherwise been monopolized (Hare and Kwetuenda 2010). Under similar circumstances chimpanzees choose to monopolize (Melis et al. 2006), while bonobos are even willing to release a stranger from another social group (Tan and Hare, 2013). This growing evidence suggests that other-regarding motivations in bonobos might be more flexible given their higher tolerance in the feeding contexts and makes them a good candidate for the prosocial choice task.

The current study, for the first time, examines the other-regarding motivations of bonobos in the prosocial choice task. To increase the intuitiveness of the task, we do not present the 1/1 and 1/0 options by using mechanical trolley system or training the subjects to associate the options with arbitrary symbols. Instead we have two human experimenters each holding a plastic tray to present and distribute the options. This social presentation method is believed and proven to be intuitive because our ape subjects regularly interact with human caretakers during feeding time (following Wobber et al. 2010b). Moreover, we conduct a rigorous self-regard pretest to make sure that each subject understands the contingency of the task *prior to* the test phase. We also vary the identity of the recipient from a familiar groupmate to an unfamiliar out-group member. Finally we manipulate the cost of the prosocial act. In the first experiment, the

subjects choose between 1/1 and 1/0. In the second experiment, the two options become 1/3 and 2/0, and any other-regard will thus incur a cost to the actor itself.

2.2.2 Experiment 1: no-cost prosociality

The experiment presents subjects with a prosocial option and an asocial option (see Figure 2.2.1a). The prosocial option, or the 1/1 option, has two slices of food with one delivered to the subject and the other to a recipient. The asocial option, or the 1/0 option, also has two slices with one delivered to the subject and the other thrown away.

Methods

Subjects

Ten bonobos (6F:4M) from Lola ya Bonobo sanctuary were tested in this experiment (Appendix D). All bonobos lived in one of three social groups with access to large forested enclosures in the day and indoor sleeping enclosures at night. Although they were orphans from bushmeat trade, it is evident that their mental health is not different from that of mother-reared bonobos (Wobber et al. 2009). Subjects could quit at any time by refusing to eat and/or sitting next to the exit of the testing rooms. Ten other bonobos participated but did not finish the pretest phases because three were uncomfortable being separated (Fizi, Lisala and Opala) and seven could not pass the pretests by the end of our field trip (Api, Kalina, Katako, Luozi, Sankuru, Tembo and

Waka). Subjects were never food-/water-deprived. To maximize subjects' motivation, the experiment was conducted prior to their morning or afternoon meal.

Each subject was paired with a recipient in the experimental trials of the test phase (see Procedure). Nine bonobos (4F:5M) played the role of the recipient and three of them were also subjects (Boyoma, Kikongo and Noiki). In five pairs, the recipient was a familiar groupmate; in the other five pairs, the recipient was a member of an out-group. The composition of the pairs was determined based on rules to maximize possible combinations and to avoid pairing individuals with known hostile relationships. To exclude potential reciprocity during the experiment, the subjects and the recipients did not reverse their roles except in the pairs of Noiki and Boyoma (due to the availability of the participants).

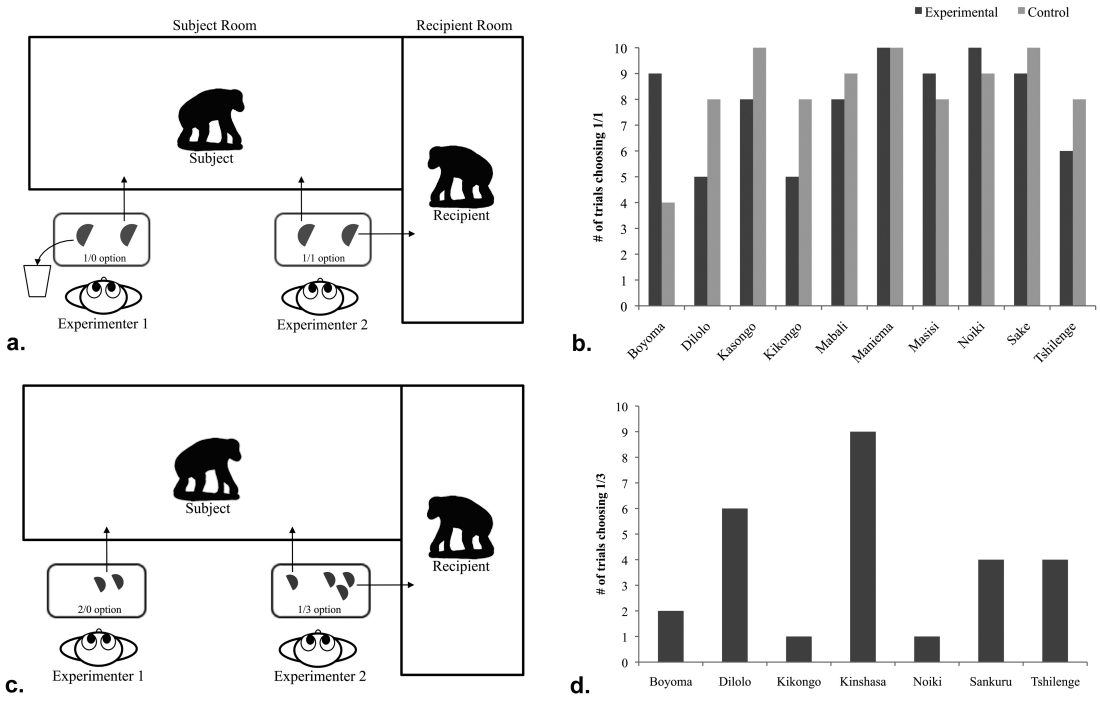


Figure 2.2.1. Setup and results of experiment 1 are shown in a) and b); setup and results of experiment 2 are shown in c) and d)

Setup

The general setup consisted of two adjacent testing rooms, the subject room and the recipient room (Figure 2.2.1a). Because the experiment was conducted in two different buildings, the sizes of the recipient rooms were slightly different (Building one: 15m^2; building two: 8.6m^2), while the size of the subject rooms was always 15m^2. The two rooms were separated by open mesh and were connected by a sliding door. Two

experimenters each held a blue, plastic tray (30x20cm) in front of the subject room to present food. They were two meters apart and their behaviors were coordinated so that subjects could never reach both simultaneously (see Procedure). Therefore, we created a contingent task that subjects could only choose one tray. Fruit slices (bananas or apples) were used as reward.

Procedure

The experiment consisted of four phases: number pretest, experience pretest, self-regard pretest and test. Each phase followed the general procedure with two experimenters (E1, E2) holding and controlling the food trays as well as a third experimenter (E3) centering the subject. A trial began as E3 lured the subject to the middle point between E1 and E2 with milk or peanuts. E1 and E2 simultaneously showed the contents of the food trays by holding them in front of the subject and calling its name for three times. They then quickly pushed the trays aside to two predetermined locations that were 2m apart and right next to the mesh. The subject had 60s to make a choice. The holder of the chosen tray distributed the food according to the rules of specific phases; meanwhile the other experimenter immediately retracted the other tray. A trial was repeated if the subject did not make a choice within 60s or if it was not centered when making a choice.

Number pretest. This phase was designed to test whether the subjects could choose between the contents of the food trays. The subjects were individually tested in the subject room. In each trial, one tray contained one slice of food while the other had two slices. The quantities of food on the two trays were switched every trial, and the locations of E1 and E2 were switched every other trial. The subject was directly handed all the food on the chosen tray. The subject could proceed to the next phase if they made correct choices in 8 out of 10 consecutive trials. The average number of trials needed was 18.10±2.28 (10-28 trials).

Experience pretest. This was a four-trial session designed to introduce the 1/0 option to the subjects. This phase was identical to the number pretest with three major exceptions. First, an opaque bucket would be placed next to the experimenter who was at the distal side of the recipient room. The bucket was out of the subject's reach and was shown to the subject that it was empty at the beginning of this pretest. Therefore, one tray was proximal to the recipient room (a.k.a. the recipient tray) and the other was proximal to the bucket (a.k.a. the bucket tray). Second, the bucket tray represented the 1/0 option. It always contained two slices of food but only delivered one slice to the subject if chosen. The holder picked up the first slice, showed it to the subject, called its name twice to attract attention, dropped that slice into the bucket, and then gave the second slice to the subject. The recipient tray was always empty to make sure that the subject would pay attention to the bucket tray. Third, the locations of the recipient tray

and the bucket tray did not change within subjects but were counterbalanced between subjects. E1 and E2 switched locations every trial. One subject (Dilolo) did not participate in this pretest because we directly administered the trials of the next phase by mistake, but this subject did experience the 1/0 option at least four times during the next phase (see below).

Self-regard pretest. This phase was designed to demonstrate that the subject understood the contingency of the task. In this pretest, the door connecting the subject room and the recipient room was open, allowing the subject to freely travel between both rooms. Like the experience pretest, the bucket tray contained two slices of food and only one slice would be given to the subject (1/0). Here the recipient tray also contained two fruit slices and represented the 1/1 option. The experimenter showed the first slice to the subject, called the subject's name twice to attract attention, dropped that slice in the recipient room, and directly handed the second slice to the subject. Therefore, the recipient tray gave the subject both slices, one in the subject room and the other in the recipient room. The locations of the two trays were consistent with the experience pretest and counterbalanced between subjects. E1 and E2 switched locations every trial. The subject could proceed to the next phase if they chose the recipient tray in 8 of 10 consecutive trials. The average number of trials needed was 12.40±1.94 (8-25 trials).

Test. This 20-trial session consisted of two types of trials. The first and the last five trials were control trials, while the 10 trials in the middle were experimental trials. The

contents and locations of the food trays were identical to the self-regard pretest, but the door connecting the subject room and the recipient room was closed. In the experimental trials, a recipient was in the recipient room (see Figure 2.2.1a); in the control trials, the recipient room was empty. Because the subject could not enter the recipient room, it received only one slice no matter which tray it chose. However, in the experimental trials choosing the recipient tray would donate one slice to the recipient (i.e. the prosocial option) while choosing the bucket tray would leave the recipient with nothing (i.e. the asocial option).

Coding and analysis

A choice was coded if the subject (1) sat right in front of one tray or (2) stuck out fingers, lips or straws toward one tray through the mesh. We also coded the recipient's positioning behavior. The recipient was in proximity to the subject room if it was right next to the mesh separating the two rooms when the subject was making a choice. We did not code gestures of the recipient due to the narrow mesh of some testing rooms that blocked gestural attempts. Intercoder reliability was high (choice: Cohen's kappa = 1; proximity: kappa = 0.890). All statistics were non-parametric and two-tailed.

Results

Figure 2.2.1b demonstrates the main results of experiment 1. The subjects preferred the 1/1 option to the 1/0 option in both the experimental and the control conditions (experimental: *Mean* = 7.90±0.60, $N = 10$, $p = 0.011$; control: *Mean* = 8.40±0.56, $N = 10$, $p = 0.006$, one-sample Wilcoxon signed rank test, two-tailed). However, their preferences for the 1/1 option did not differ between the two conditions throughout the test phase, in the first 5 or in the last trials (overall: $N = 10$, $Z = 1.018$, $p = 0.309$, one tie; first 5 trials: $N = 10$, $Z = 0.144$, $p = 0.885$, two ties; last 5 trials: $N = 10$, $Z = 1.228$, $p = 0.219$, three ties; all Wilcoxon signed rank test, two-tailed). In either condition, the subjects' preferences did not change when the first 5 and the last 5 trials were compared (experimental: $N = 10$, $Z = 0.333$, $p = 0.739$, four ties; control: $N = 10$, $Z = 0.966$, $p = 0.334$, five ties, Wilcoxon test, two-tailed). At the individual level, in each condition there were five subjects choosing the 1/1 option for 9 or 10 times ($p < 0.05$, binomial test, two-tailed, see Figure 2.2.1b). However, no subject showed a prosocial preference by choosing the 1/1 option more often in the experimental condition than in the control condition, but one subject, Boyoma, did show a prosocial tendency ($p = 0.057$, Fisher's exact, two-tailed).

We scored the difference in the frequency of choosing the 1/1 option between the experimental and the control condition as a measure of each subject's prosociality. The subjects' sex, the recipient's sex, location and group membership had no effect on this difference score (the subjects' sex: $N = 10$, $U = 8$, $p = 0.388$; the recipient' sex: $N = 10$, $U =$

10.5, $p = 0.746$; the recipient' location: $N = 10$, $U = 9.5$, $p = 0.526$; the recipient' group membership: $N = 10$, $U = 9.5$, $p = 0.526$; Mann-Whitney U test, two-tailed). No correlation was found between this difference score and the estimated age of the subjects ($N = 10$, $r = -0.356$, $p = 0.312$, Spearman's correlation, two-tailed). In the experimental trials, the subjects' choices did not correlate with whether the recipient was close to the separation mesh ($N = 100$, $r = 0.099$, $p = 0.321$, Phi coefficient, two-tailed).

Discussion

Although the subjects preferred the prosocial option to the asocial option when the recipient was present, they showed the same preference when the recipient was absent. The individual analysis is consistent with this pattern by showing that half of the subjects preferred the 1/1 option even in the control condition. This result suggests that the subjects have developed a general bias toward the content and/or the location of the 1/1 option.

It is unlikely that the subjects were simply attracted by the content of the 1/1 option because both options always contained two pieces of food. Alternatively, the subjects might have preferred the 1/1 option in an attempt to retrieve the fruit slice delivered into the recipient room even though they had no access. However, they were tested in their sleeping building and thus understood the separation caused by the sliding door. Moreover, this scenario would predict the subjects chose the 1/1 option *less*

often in the experimental trials because there was a recipient to consume the first fruit slice.

It is likely that this bias was toward the location of the 1/1 option induced by the self-regard pretest because the subjects were required to choose the 1/1 option 8 of 10 times before the test phase. Our results were consistent with the chimpanzee prosocial choice experiments with a proper self-regard pretest (Jensen et al. 2006, experiment 1; Yamamoto and Tanaka 2009, experiment 1). In the experiment 1 of Jensen et al. (2006) that had a similar lateral setup of the two options, their chimpanzee subjects had a pre-existing bias toward the location of one option; in the experiment 1 of Yamamoto and Tanaka (2009), their chimpanzees were trained to associate each option with a button in a fixed color, and they developed a bias toward one particular button/color. However, in other studies with non-ape primates, a self-regard pretest did not result in such a bias (capuchins: Lakshminarayanan and Santos, 2006; tamarins: Cronin et al. 2009; marmosets: Burkart et al. 2007). It seems like this bias developed only when the two options were counterbalanced between subjects (in contrast to within subject). All these non-ape studies utilized a two-tiered apparatus with one food tray locating above the other, which allowed the location of the 1/1 option to be easily counterbalanced within subject. In contrast, both Jensen et al. and the current experiment placed the two food trays side by side. Due to the logistical difficulty of moving the subjects around testing rooms, this lateral arrangement presumably prevented within-subject counterbalancing

and allowed a location cue to be always associated with the 1/1 option since the self-regard pretest. This association might be particularly easy given that both options yielded equal payoff to the subjects. As a result, the subjects showed a carry-over bias toward this location/option in the test. Similarly in the experiment 1 of Yamamoto and Tanaka (2009), the trained association between the outcome of one option and the button in a specific color might have precluded within-subject counterbalancing and led to a color bias.

One solution to avoid this bias is to make the location of the prosocial option opposite to the biased option so that the actor has clearly overcome this bias if any prosociality were observed (see also Massen et al. 2010, Horner et al. 2011). In the second experiment, we thus adjusted the reward distributions: the prosocial option would deliver one fruit slice to the subjects and three slices to the recipient room (1/3); while the other option would have only two pieces and would all go to the subjects (2/0). In the self-regard pretest, the subjects would have to prefer the 2/0 option to understand they would obtain less food if the 1/3 option were chosen, but in the test, the subjects would need to choose the 1/3 option to benefit the recipient. As a result, we also created a costly sharing situation where the prosocial act could be regarded as altruistic.

2.2.3 Experiment 2: costly prosociality

The experiment presents subjects with an asocial option and a prosocial option (Figure 2.2.1c). The asocial option (the 2/0 option) has two slices of food that would all be given

to the subjects; while the prosocial option (the 1/3 option) has four slices with one delivered to the subjects and three to the recipient.

Methods

Subjects

Seven bonobos (4F:3M) participated in this experiment that was conducted in parallel with experiment 1. Five of them were subjects in experiment 1 (Appendix E). Four other bonobos were dropped out of the experiment because they were not able to pass the pretests by the end of our field trip (Mabali, Maniema, Muanda and Tembo). Each subject was paired with a recipient that was from the same social group. Five bonobos played the role of recipient and three of them were also subjects (Kikongo, Noiki and Tchilenge). We followed the same rules as in experiment 1 to determine the pairings. There was no role-reversal except in the pairs of Kikongo and Tchilenge due to the availability of the participants.

Setup and Procedure

Figure 2.2.1c shows the setup of the current experiment. Its setup and general procedure were identical to experiment 1 with two food trays and three experimenters. This experiment consisted of four phases: number pretest I, number pretest II, self-regard pretest and test.

Number pretest I. This phase was designed to test whether the subjects could choose between the contents of the food trays and prefer two slices to one slice. It was identical to the number pretest in experiment 1. The subject could proceed to the next phase if they made correct choices in 8 of 10 consecutive trials. The average number of trials needed was 16.14±2.42 (10-26 trials).

Number pretest II. This phase was designed to test whether the subjects would prefer four fruit slices to two. It was identical to the number pretest I except that one tray contained two slices and the other contained four. Subjects needed on average 10.14±0.51 (9-13) trials to pass this phase.

Self-regard pretest. This phase was designed to introduce the 1/3 and the 2/0 options in the test phase and demonstrate that the subjects understood the payoff of each option. In this phase, the recipient room was empty and was separated from the subject room by open mesh. The recipient tray was the 1/3 option and always contained four fruit slices. If the subjects chose this tray, the holder picked up three slices, showed them to the subject by calling the subject's name twice, dropped them into the recipient room and directly gave the last slice to the subject. The subject could see but could never retrieve the food in the recipient room, which yielded a 1/3 payoff. The other tray contained two slices and all would be delivered to the subject if it were chosen, which yielded a 2/0 payoff. The location of the recipient room did not change within subject but was counterbalanced between subjects. The two tray-holders switched locations

every trial. To demonstrate an understanding of the two options, the subject had to choose the 2/0 option in 8 of 10 consecutive trials. The average number of trials needed was 28.43±4.12 (16-46 trials).

Test. This 10-trial session was identical to the self-regard pretest except that there was a recipient in the recipient room. The test was conducted no more than one day after the self-regard pretest. The locations of the two options were the same as the self-regard pretest. Therefore, choosing the 1/3 option was altruistic because it benefited the recipient at a cost to the subject. Moreover, an altruistic choice would require the actor to overcome any location bias toward the 2/0 option established in the self-regard pretest.

Coding and Analysis

All coding followed the same criteria as in experiment 1. All statistics were non-parametric and two-tailed. Interobserver reliability was perfect (choice: Cohen's kappa = 1; proximity: kappa = 1).

Results

As shown in Figure 2.2.1d, the subjects as a group chose the two options randomly in the test (*Mean* = 3.86±1.10, *N* = 7, *p* = 0.303, one-sample Wilcoxon signed rank test, two-tailed). They did so in the first and the second half of the test (first half: *Mean* = 2.14±0.55, *N* = 7, *p* = 0.391; second half: *Mean* = 1.71±0.57, *N* = 7, *p* = 0.200, one-sample Wilcoxon

signed rank test, two-tailed). At the individual level, two subjects (Noiki and Kikongo) preferred the 2/0 option while one subject (Kinshasa) preferred the 1/3 option (all p = 0.021, binomial test, two-tailed).

The subjects' sex, the recipients' sex and the location of the recipient room did not affect the likelihood of choosing the 1/3 option (the subjects' sex: N = 7, U = 4.5, p = 0.589; the recipients' sex: N = 7, U = 6, p = 1.000; the location of the recipient room: N = 7, U = 4.5, p = 0.589; Mann-Whitney U test, two-tailed). The estimated age of the subjects also had no effect (N = 7, r = -0.315, p = 0.492, Spearman's correlation, two-tailed). Unlike experiment 1, the subjects' choice of the 1/3 option, however, was correlated with the proximity of the recipient (N = 70, r = 0.262, p = 0.029, Phi coefficient, two-tailed).

Discussion

The subjects did not prefer the 2/0 option as a group, although two individuals did show such a preference. The subjects likewise did not prefer the 1/3 option with one individual exception. It is plausible that the subjects at least demonstrated some degree of prosociality because they did not overwhelmingly choose the 2/0 option. Consistent with this interpretation, the correlation between the proximity of the recipient and the altruistic choice of the subjects might suggest that the subjects responded to the recipient's desire for food signaled by its proximity to the mesh (Warneken et al. 2007, experiment 3). Alternatively, the subjects might have been affected by local

enhancement, i.e. they were socially attracted by the presence of the recipient so that they did not exclusively choose the 2/0 option during the test.

2.2.4 General Discussion

The two experiments are the first attempt to examine other-regarding motivations of bonobos in the prosocial choice paradigm validated by a self-regard pretest. In the first experiment, the subjects could benefit the recipient by making a prosocial choice at no cost to themselves, but they showed a preference for the prosocial option regardless of the presence of the recipient. Their choices seemed to be determined by a bias toward the location of the prosocial option. In the second experiment, the subjects would have to overcome this location bias to benefit the recipient and they would also obtain less food by doing so. However, they showed no preference for any option or location. Although this might be taken as weak evidence of other-regarding motivations, we could not rule out lower level explanation such as local enhancement.

Overall our experiments with bonobos show little evidence of other-regarding motivations in the prosocial choice task. Our findings are consistent with the null results from chimpanzee experiments with a self-regard pretest (Jensen et al. 2006, experiment 1; Yamamoto and Tanaka 2009, experiment 1). One possible reason is methodological. As discussed above, the side-by-side arrangement of the two options possibly precluded within-subject counterbalancing and resulted in a location bias that overshadowed subjects' other-regarding motivations. To corroborate, the subjects did show some signs

of other-regards when the subjects were forced to counter this bias to make a prosocial choice in experiment 2. Moreover, a vertical arrangement used in other studies allowed within-subject counterbalancing and those animals did not develop a location bias during the self-regard pretest (Burkart et al. 2007, Cronin et al. 2009, Lakshminarayanan and Santos 2006). We believe that one must demonstrate self-regard before attempting to show other-regard, and the design of future studies should counterbalance the two options within subject to avoid any potential bias induced by the necessary self-regard pretest.

The current findings are inconsistent with our instrumental helping study with the same bonobo population (Tan and Hare 2013). In that four-experiment study, bonobos are willing to not only help a recipient (a groupmate or a stranger) obtain out-of-reach food but also voluntarily share monopolizable food with the recipient (Tan and Hare, 2013). However, this discrepancy echoes experiments showing the same chimpanzees are indifferent in the prosocial choice task but helpful in the instrumental helping task (Yamamoto and Tanaka 2009, Yamamoto et al. 2010, 2012). Therefore, other-regarding motivations in bonobos and chimpanzees might, therefore, seem more similar than suggested by their apparent contrast in social tolerance.

This similarity raises three questions open to future studies. First, what are the psychological consequences of high-level social tolerance if other-regarding motivations were not one of them? It is possible that the social tolerance in bonobos does not result in

a stronger predisposition of unselfishness, but rather it extends prosocial behaviors (selfishly or unselfishly motivated) to a boarder range of recipients from kin and friends to strangers (Tan and Hare 2013). Second, what drove the evolution of other-regarding motivations if it was not (only) driven by high-level social tolerance? Could it be cooperative breeding (Burkart et al. 2009) or collaborative foraging (Hamann et al. 2011)? Third, does food transfer in the prosocial choice task represent a key gap between humans and nonhuman apes? So far only one study has been conducted to validate the prosocial choice paradigm in humans (Brownell et al. 2009). However, it did not conduct a self-regard pretest and adopted a very different design (i.e. instead of comparing between a recipient-present and a recipient-absent condition, it compared between an experimental condition where the recipient was expressing desires for food and a control where the recipient remained passive). We believe that the use of comparative methods across humans, chimpanzees, bonobos and other target species of theoretical importance are necessary to eventually identify the variation and the origin of other-regarding motivations (see MacLean et al. 2011).

2.3 Study 3: Do bonobos attach positive valence to strangers? [3]

2.3.1 Introduction

[3] Reprinted from manuscript, Tan J & Hare B, in prep, Bonobos are xenophilic.

It is an evolutionary puzzle that humans regularly interact with strangers in a prosocial way (Seabright 2004, Sterelny 2011). This prosociality toward strangers likely has a biological basis because it is widespread across different cultures (Henrich et al. 2005, 2006), is partially heritable (Cesarini et al. 2008, Wallace et al. 2007) and has an early ontogeny (Warneken & Tomasello 2006, 2012). From a functional perspective, it is difficult for prosocial actors to receive selfish benefits from strangers through inclusive fitness, reciprocal exchange, punishment or even reputation (Fehr & Fischbacher 2003, Gintis et al. 2008). From a phylogenetic perspective, although a growing number of primate species are found to voluntarily help or share with familiar individuals (see de Waal & Suchak 2010, Hare & Tan 2011, Cronin 2012), nonhuman primates are in general territorial and xenophobic due to intergroup competition (Crofood & Wrangham 2010). This puzzling human phenomenon has thus lead many to propose that humans have evolved unique prosocial motivation toward strangers (Burkart et al. 2009, Silk & House 2011, Cheney 2011).

Bonobos (*Pan paniscus*) provide a powerful test of this uniqueness hypothesis because they are known for high levels of intergroup tolerance. Observations of both wild and captive bonobos demonstrate that they are capable of having peaceful interactions with strangers (Gold 2001, Pfalzer et al. 1995, Furuichi 2011). Lethal intergroup aggression has never been reported in any bonobo populations (Hare et al. 2012, Wrangham 1999). Instead, affiliative behaviors such as grooming, co-feeding and

sexual behaviors are frequently observed during intergroup encounters in the wild and during introduction of new individuals in captivity (Idani 1990, 1991, Hohmann & Fruth 2002, Furuichi 2011, Gold 2001, Pfalzer et al. 1995). These observational studies suggest the possibility that in most primates prosociality toward strangers is constrained by xenophobia and a species with high level of intergroup tolerance such as bonobos might be capable of prosocial behavior toward strangers.

Two recent experimental studies directly challenge the uniqueness hypothesis by showing that bonobos voluntarily share food with strangers (Hare & Kwetuenda 2010, Tan & Hare 2013). In a food-sharing task, bonobos entered a room with a pile of desirable food and they could either monopolize or release a locked recipient into the room to share the food. Bonobos not only chose to share, but also preferred sharing with a stranger from another social group to a known bonobo from their own group (Hare & Kwetuenda 2010, Tan & Hare 2013). When the subject made a direct choice between sharing with a groupmate and a stranger, the xenophilic preference was so strong that after the subject first released the stranger, the stranger went to release the third bonobo (i.e. the groupmate recipient, Experiment 1, Tan & Hare 2013). Because the third bonobo and the subject were from the same group, the stranger voluntarily let herself be outnumbered by two bonobos from an outgroup. This observed sharing is in part driven by a strong motivation to initiate a physical interaction with strangers. In a follow-up experiment, bonobos became unwilling to share food with the stranger if they were

always separated and had no chance to release the stranger in the same room (Experiment 4, Tan & Hare 2013).

These findings of bonobos support the first impression hypothesis that prosociality toward strangers can evolve in species with intergroup tolerance and is a way to extend one's social network. According to the hypothesis, the cost of social network extension is relatively low in bonobos due to their reduced risk of interacting with strangers and relaxed feeding competition (Hare et al. 2012, Wrangham 1999). As a result, bonobos can reap the benefits of starting a new social relationship such as inbreeding avoidance (Pusey & Wolf 1996, Furuichi 2011), cooperation (Noë & Hammerstein 1994, Hare et al. 2007) and/or stress reduction (Taylor et al. 2000, Sapolsky 2005). A physical interaction with strangers is so desirable that bonobos are willing to facilitate it by forgoing food that otherwise would not be shared. In corroboration, bonobos did not share food in their possession when the recipient was a groupmate (Tan & Hare 2013, see also Bullinger et al. 2012, Jaeggi et al. 2011).

One core prediction of this hypothesis is that bonobos will seek to initiate a social interaction with strangers in other contexts even when food sharing is not required. This social engagement process brings two strangers into close proximity peacefully and therefore becomes the first step to establish a new relationship (Porges 2003, Carter & Porges 2010, Taylor et al. 2000). To allow for social engagement, a necessary psychological factor is xenophilia, or a positive appraisal of the event of encountering

strangers (Ellsworth & Scherer 2003). More specifically, during the encounter strangers should, by default, be perceived or evaluated as a social stimulus of positive valence that is not only safe but also desirable (Porges 2003). This psychological mechanism is similar to findings in social psychology that humans universally tend to use perceived warmth as a primary dimension to categorize others (see Fiske et al. 2006).

However, to our knowledge there remains no study testing this psychological prediction of the first impression hypothesis in bonobos. The goal of the current study is thus to examine whether bonobos attribute positive valence to strangers. To measure valence, we use an involuntary task, contagious yawning, and a voluntary choice task, social valuation. In addition, strangers in the current study are bonobos from the Columbus Zoo in Ohio, USA. This is a group of bonobos that are completely unfamiliar to the subjects living in Kinshasa, Democratic Republic of Congo. In previous studies, strangers were from neighboring groups and could have had prior communications through visual or vocal contacts (Hare & Kwetuenda 2010, Tan & Hare 2013). The current design thus allows a true measure of first impression.

The first task measures the contagiousness of yawning, a stereotypic behavior with limited voluntary control (Provine 2005). Contagious yawning refers to yawning behavior that is elicited by the visual (and sometimes auditory) exposure to yawning of others (Provine 1986, 2005). This phenomenon has been observed in a number of social primates (humans: Provine 1986, Platek et al. 2003, Norsica & Palagi 2011; bonobo:

Demuru & Palagi 2012; chimpanzee: Anderson et al. 2004, Campbell et al. 2009, Campbell & de Waal 2011, Massen et al. 2012; gelada baboon: Palagi et al. 2009; stumptail macaque: Paukner & Anderson 2006). Contagious yawning might have a communicative function (Daquin et al. 2001, Guggisberg et al. 2010), because it has also been reported in other social animals such as domestic dogs (Joly-Mascheroni et al. 2008, Harr et al. 2009, O'Hara & Reeve 2011, Silva et al. 2012, Madsen & Presson 2013) and perhaps budgerigars (Gallup et al. 2009), but not solitary red-footed tortoises (Wilkinson et al. 2011).

Although the proximate mechanism of contagious yawning remains unclear, current hypotheses predict that it measures the perceived valence of the yawner. The empathy hypothesis argues that contagious yawning is caused by the automatic acquisition of an emotional state as a result of the perception of the similar state expressed in others (defined as "emotional contagion" or "empathy", Bernhardt & Singer 2012, Decety & Svetlova 2012, Preston & de Waal 2002, de Waal 2008). This hypothesis predicts that the matching of emotional states is easier between dyads with high level of social closeness (Preston & de Waal 2002, de Waal 2008). The mimicry hypothesis proposes that contagion is caused by unconscious mimicry of the motor pattern of a yawn (Yoon & Tennie 2010, Chartrand & van Baaren 2009). Mimicry is "social glue" that increases the affiliation between the mimicker and the model (Chartrand & Bargh 1999, Lakin & Chartrand 2003, Paunker et al. 2009) and occurs more

often when the mimicker likes or wants to affiliate with the model (Lakin & Chartrand 2003, Lakin et al. 2008, McIntosh 2006). As a result, it is clear that both hypotheses predict that the occurrence of contagious yawning is a reliable signal of positive valence. Empirical research supports this prediction. Yawning is more contagious among individuals with stronger social bonds in various primate species, including bonobos (Norsica & Palagi 2011, Demuru & Palagi 2012, Palagi et al. 2009, but see Massen et al. 2011). In chimpanzees, contagious yawning occurs between groupmates but it is absent between strangers (Campbell & de Waal 2011). This is consistent with the natural history of chimpanzees that are known for strong xenophobia and lethal aggression toward strangers (Wilson & Wrangham 2003, Muller & Mitani 2005).

The first experiment of the current study tests if yawning in bonobos is contagious between strangers. It also examines whether yawning is more contagious between groupmates or between strangers. Based on the first impression hypothesis and previous findings of bonobo xenophilia (Hare & Kwetuenda 2010, Tan & Hare 2013), we predict that bonobos will yawn contagiously with strangers, and the yawns of strangers will be as or more contagious than the groupmates' yawns.

The second experiment measures how bonobos evaluate the opportunity to watch video stimuli of strangers and groupmates. In both humans and nonhuman primates, visual stimuli of others have intrinsic valence that varies in dimensions important to survival and reproduction (Anderson 1998, Deaner et al. 2005, Mahajan et

al. 2011, Rohdes 2006). To gain visual access to social stimuli with positive valence (e.g. high-status individuals or attractive mates), humans and monkeys are willing to pay a cost in the form of food, time or effort (Aharon et al. 2001, Deaner et al. 2005, Hayden et al. 2007). These findings suggest that primates are able to value social stimuli in terms of their adaptive valence. Similar social valuation tasks, therefore, can also be used to measure the default valence of strangers.

Following Rosati and colleagues (2007), the second experiment is essentially a temporal discounting task in which subjects choose between a small, immediate food reward and a large, delayed food reward. In Rosati et al., the subjects simply had to stay in the testing room and wait for the reward if they chose the delay option. In the current design, the subjects can watch a video of another bonobo during the waiting period. The content of the video will be the headshot of a groupmate or a stranger. If a video stimulus has a positive valence, it will increase the subjects' likelihood of choosing the delayed reward; if the stimulus contains negative valence, it will decrease the value of the delayed reward. Therefore, this social valuation experiment measures how much the subjects are willing to pay an opportunity cost (i.e. time) to watch a social stimulus. The first impression hypothesis predicts that bonobos are more willing to watch the stranger videos than the groupmate videos.

2.3.2 Experiment 1: contagious yawning

Methods

Subject

As listed in Appendix F, twenty-five bonobos (12F:13M) participated in the current study. Their estimated ages were between 3 and 18. Seventeen subjects were considered adults (age ≥ 7, based on the age of sexual maturity in captive bonobos, Tan & Hare 2013). These bonobos were orphans from bushmeat trade and were living in social groups in Lola ya Bonobo sanctuary, Kinshasa, Democratic Republic of Congo. A comparison found no substantial differences in psychological health between these orphans and mother-reared individuals (Wobber et al. 2011). Three female bonobos (Lukuru, Kananga, Lisala) only finished the stranger conditions and one male bonobo (Kasongo) only finished the groupmate conditions. Lukuru and Kananga lived in a small group that did not have enough individuals to produce the groupmate stimuli. The groupmate conditions of Lisala and the stranger conditions of Kasongo were aborted because they were shown the videos in the wrong order. This experiment was conducted in November 2011.

Stimuli

We adopted a 2×2 design that yielded four different conditions (stranger-experimental, stranger-control, groupmate-experimental, groupmate-control). In the groupmate conditions, the subjects watched a sequence of video clips showing face-

shots of bonobos from the subjects' social groups. In the stranger conditions, the video clips showed bonobos from Columbus Zoo (Ohio, USA) whom the subjects have never met before. The experimental sequences contained clips each showing a complete yawn of a model bonobo and the control sequences contained clips showing the same bonobos resting with no facial expression. Because yawning sometimes signals stress (Baenninger 1997, Maestripieri et al. 1992), we recorded all videos in the context of resting. Each sequence lasted for approximately two minutes and contained 12 clips from six adult bonobos (3F:3M, two clips per bonobo). The order of clips in each sequence was fixed: three male clips, three female clips, three males, and three females. For the subjects who were also model bonobos in the clips, their clips were removed from the sequence. These subjects would watch 10-clip sequences in the groupmate conditions, but they would still be exposed for the same amount of time as in the stranger conditions (see Procedure).

Each clip lasted for 6-16 seconds and started with a 2-second attention-getter (i.e. a bright yellow screen and a ringing sound). Besides the ringing sound, the clips were silent. In each clip there was only one bonobo. Experimental and control clips were extracted from the same source videos. They were thus matched in playing order, video length, brightness, contrast, the model's identity and its body posture. All stimuli were in .AVI format with a 720×540 resolution.

Setup

The subjects were tested in their sleeping dormitories. For subjects from group 1 and 3, their testing room was 2 m × 4 m. For subjects from group 2, the room was 3 m × 4 m. We presented the video stimuli to the subjects with three synchronized 8″ digital photo frames (NIX™ Pro-Series). These screens were set up outside the testing room and on the same side. The distance between the screens and the mesh was 90 cm. Two screens were placed on wooden tables 80 cm above the ground and 1-1.5 m between each other. The third screen was mounted on a metal rack that stood 1.6 m above the ground and in the midpoint of the two lower screens. The screens were controlled by a single remote. Therefore, we created a "wall" of synchronized screens so that the subjects would be exposed to the stimuli whenever they were looking at that side of the testing room.

Experimenter 1 (E1) and 2 (E2) each held a camera (JVC and Sony HandyCam HDR-XR200V) to videotape the experiment from two different angles. For subjects from group 1 and 3, E1 was videotaping from the side and E2 was opposite the screens. For subjects from group 2, E1 was recording from behind the screens and E2 was at the side.

Procedure

The subjects were tested alone (N=17), with an infant (N=7) or with an adult companion (N=1). The experiment included 4 one-session conditions (see Stimuli). Each

subject participated in two testing days and received two testing sessions with the same model bonobos each day. The two testing days were at least 5 days apart. The order of conditions was counterbalanced between subjects.

Each session lasted for 15 minutes and consisted of two phases, a playing and a watching phase. The 5-minute *playing phase* was designed to increase and, therefore, control the arousal state of the subjects within a testing day. This was because 1) we conducted the experiment early in the morning when the subjects might be so sleepy that they would yawn at a ceiling level, and 2) we conducted two sessions per day so that the first session might have a carry-over effect on the second one. In this phase, an experimenter was grooming and feeding the subjects. Immediately after was the 10-minute *watching phase* in which the experimenters started the videos and passively videotaped the subjects. The stimulus sequence was repeated throughout the session so that the subjects have been exposed for the same amount of time across sessions. The second session immediately followed the first one.

Coding and analysis

A *yawn* was coded when the subjects made a slow gaping movement that was not in the context of feeding, vocalizing or playing. To measure the strength of yawn contagion, a *contagion score* was calculated as the difference in the number of yawns between the experimental and the control condition on the same testing day. Yawning

latency referred to the time between the start of the watching phase and the onset of the first yawn observed. In addition, we considered an individual as adult if its age was seven or above (based on the estimated age of sexual maturity in captive bonobos, Tan & Hare 2013). A second coder blind to the testing condition coded 20% randomly selected trials. Inter-coder reliability was excellent (number of yawns: $N = 18$, $r = 0.981$, $p < 0.001$; latency: $N = 12$, $r = 1.000$, $p < 0.001$, Spearman's correlation, two-tailed).

Results

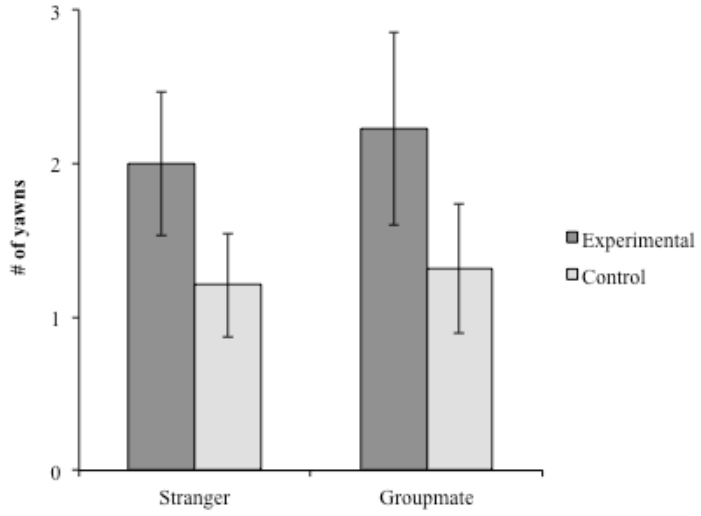


Figure 2.3.1 Overall results of experiment 1.

Figure 2.3.1 shows the overall results of the current experiment. We conducted a 2 (treatment: experimental versus control condition) × 2 (membership: stranger versus

groupmate) repeated measures ANOVA with sex (male versus female) and age-group (adult versus non-adult) as between-subject variables. We chose sex as a between-subject variable based on observed sex difference in baseline yawning rates in other primates (Deputte 1994, Hadidian 1980, Troisi et al. 1990). We chose a binary age-group variable because previous studies in *Pan* only found contagious yawning in adults (Anderson et al. 2004, Campbell & de Waal 2009, 2011, Massen et al. 2012, Demuru & Palagi 2012). The analysis revealed a main effect of treatment ($F_{1,17}$ = 9.023, p = 0.008), showing that subjects yawned more when they were watching yawning stimuli than control stimuli. The analysis also found a marginally significant treatment × age-group interaction ($F_{1,17}$ = 3.866, p = 0.066) and a significant membership × treatment × age-group interaction ($F_{1,17}$ = 9.988, p = 0.006). No other effect or interaction was found to be statistically significant. We conducted pairwise comparisons to further analyze these results. First, we considered all subjects together. Overall subjects showed contagious yawning in the stranger conditions but not in the groupmate conditions (stranger: N = 24 (eight ties), Z = -2.177, p = 0.029; groupmate: N = 22 (seven ties), Z = -1.172, p = 0.241, Wilcoxon test, two-tailed). However, the contagion scores did not differ between the stranger and the groupmate conditions (N = 21 (four ties), Z = -0.333, p = 0.739, Wilcoxon test, two-tailed). Latency analysis showed that subjects yawned neither earlier nor later in the experimental condition than in the control (stranger: N = 10 (no ties), Z = -1.172, p = 0.241; groupmate: N = 6 (no ties), Z = -0.524, p = 0.600, Wilcoxon test, two-tailed). Irrespective of

the membership of the models, in the first testing day subjects yawned more in the experimental condition than in the control (N = 25 (seven ties), Z = -2.012, p = 0.044, Wilcoxon test, two-tailed). In the second day the subjects did not show the contagion effect (N = 21 (eight ties), Z = -1.249, p = 0.212, Wilcoxon test, two-tailed), but the contagion scores of the two days did not differ from each other (N = 21 (four ties), Z = -0.928, p = 0.353, Wilcoxon test, two-tailed).

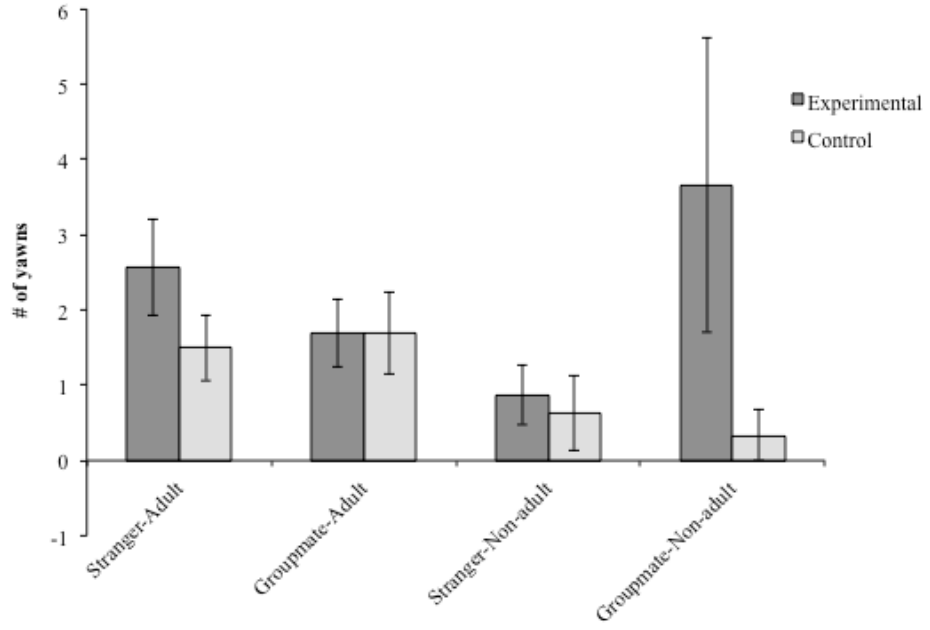


Figure 2.3.2 Results of adult and non-adult subjects in experiment 1.

Second, to further understand the three-way interaction, the two age-groups were analyzed separately (see Figure 2.3.2). Adult subjects showed contagious yawning with strangers but not groupmates (stranger: N = 16 (four ties), Z = -2.107, p = 0.035;

groupmate: $N = 16$ (four ties), $Z = -0.040$, $p = 0.968$, Wilcoxon test, two-tailed). A marginally significant difference in the contagion score was found between the stranger and the groupmate conditions. Among adult subjects, the contagiousness seems to be higher in the strangers' yawns than the groupmates' yawns ($N = 15$ (three ties), $Z = -1.901$, $p = 0.057$, Wilcoxon test, two-tailed). As a group non-adult subjects did not show contagious yawning (stranger: $N = 8$ (four ties), $Z = -0.557$, $p = 0.577$; groupmate: $N = 6$ (three ties), $Z = -1.604$, $p = 0.109$, Wilcoxon test, two-tailed). Nor did their contagion scores differ between the stranger and the groupmate conditions ($N = 6$ (one tie), $Z = -1.625$, $p = 0.104$, Wilcoxon test, two-tailed).

Third, we analyzed a subgroup of the subjects that were tested first in the groupmate conditions and last in the stranger conditions, because this was the testing order used by Campbell and de Waal (2011) to find that chimpanzees only yawn contagiously with groupmates. We again found that subjects showed yawn contagion in the stranger conditions but not in the groupmate conditions (stranger: $N = 11$ (four ties), $Z = -1.983$, $p = 0.047$; groupmate: $N = 11$ (three ties), $Z = -1.198$, $p = 0.231$, Wilcoxon test, two-tailed), although their contagion scores did not differ ($N = 11$ (three ties), $Z = -0.422$, $p = 0.673$, Wilcoxon test, two-tailed).

Finally, whether subjects were tested alone or in pairs had no effect on the yawn contagion with strangers or groupmates (stranger: $N = 24$, $U = 55$, $p = 0.570$; groupmate: $N = 22$, $U = 52.5$, $p = 0.808$, Mann-Whitney test, two-tailed).

Discussion

Experiment 1 has four main findings. First, it replicates the finding that bonobos yawn contagiously with others. Second, for adult subjects yawning is contagious among completely unknown strangers. Third, for adult subjects yawning is likely more contagious among strangers than groupmates. Fourth, for all subjects the yawns of strangers are at least as contagious as those of groupmates. What makes these results more meaningful is that it has been shown in bonobos that yawning is more contagious among dyads with positive valence (Demuru & Palagi 2012). Furthermore, the strangers in this experiment included a representative sample of males and females, and they were completely unknown to the subjects prior to the exposure. These results are consistent with the predication of the first impression hypothesis that bonobos, by default, attribute positive valence to strangers.

These results are in stark contrast to chimpanzees' ingroup-only responses in a similar contagious yawning paradigm (Campbell & de Waal, 2011). This species difference in contagious yawning adds to the growing literature that bonobos and chimpanzees have distinct psychological responses toward strangers (Wilson et al. 2001, Herbinger et al. 2009, Tan & Hare 2013, Wrangham 1999). Admittedly, qualitative comparison should be made with caution due to methodological variations across studies (Campbell & de Waal 2010). Unlike the current experiment, Campbell and

colleagues (2011) had only adult subjects and conducted the stranger conditions after the subjects finished the groupmate conditions. The absence of contagion with strangers in chimpanzees might thus be a result of age/order effect (see also Videan et al. 2005 for correlational evidence of social contagion among neighboring chimpanzees). However, this interpretation is unlikely given the detailed analysis of the current results. Bonobos again showed contagious yawning with strangers when 1) only adults were included in the analysis or 2) they were tested in the groupmate conditions first. Therefore, the specie difference stands even when the potential methodological differences are controlled.

Another result is that the subjects might have become habituated to the exposure on the second testing day even though after an interval of at least five days. We found that testing the subjects alone or in pairs did not affect the results. The sex of the subjects also has no effect on contagious yawning. To our knowledge, no studies on contagious yawning in primates have found an effect of the subjects' sex. However, the sex of the models seems to influence contagion (Demuru & Palagi 2012, Massen et al. 2012, Palagi et al. 2009). Future studies should explore the potential interplay between the sex and the membership of the models.

One possible alternative to the current results is that yawning is a stress response to perceived threats. This negative-valence interpretation argues that yawning exposes canines that might be perceived as threatening displays (Redican 1975). Because

yawning is a quite reliable indicator of stress in nonhuman primates (Baenninger 1997, Maestripieri et al. 1992), the subjects' contagious yawning might be a stress response to a stimulus of negative valence. We disagree with this argument for four reasons. First, yawning is not a signal of threats because the majority of yawns occur in contexts unrelated to aggression (e.g. resting) and canine-displaying behaviors in general are not followed by aggressive behaviors (Baenninger 1997, Dobson 2010). Second, even though the *occurrence* of a yawn might be linked to a change of arousal states including stress and anxiety, it does not contradict the findings that the *contagion* of a yawn is linked to social affiliation (Norsica & Palagi 2011, Demuru & Palagi 2012, Palagi et al. 2009, Campbell & de Waal 2011). Third, all the yawning stimuli were recorded in peaceful, resting contexts and were thus unlikely to be stress yawns. Fourth, we would expect chimpanzees to yawn more with strangers than groupmates if yawn is a stress response.

Another unlikely alternative is that subjects were incapable of recognizing memberships from the videos. First, it is evident that adult subjects recognized the membership of the models because they yawned with strangers but not groupmates. Second, all subjects had plenty of opportunities to identify the individuals during the experiment. Each stimulus sequence contained 12 different video clips of six bonobos and these clips have been repeatedly exposed to the subjects for 10 minutes. Third, bonobos are capable of individual recognition in other contexts (Tan & Hare 2013). To further test this alternative, experiment 2 presents subjects a voluntary choice to watch

two sets videos (groupmates and strangers). Importantly, those videos will be presented in the same device, format and resolution as experiment 1. If the subjects show preference for any set of videos, it suggests that they are capable of discriminating memberships from the videos.

2.3.3 Experiment 2: social valuation

In the current experiment, we use the social valuation task to achieve two goals. The first goal is to use a different paradigm measuring voluntary choice to test the prediction of the first impression hypothesis that bonobos attribute positive valence to strangers. The secondary goal is to test if the subjects are capable of identifying memberships from the videos.

Methods

Subjects

As shown in Appendix G, twenty bonobos (10F:10M) from two social groups in Lola ya Bonobo sanctuary finished the current experiment. One other female lost motivation during the introduction phase and two other male bonobos lost motivation after finishing only the groupmate condition. The experiment was conducted in November 2011 and October 2012.

Stimuli

In each testing day, the subject could choose to watch a sequence of video stimuli. These stimuli showed other bonobos' face shots captured when they were at rest and had no expression. Each clip lasted for four seconds and began with a bright yellow fixation screen and a ringing sound as attention getters. Besides the ringing sound, the clips were silent. All clips were formatted to .AVI and 720 × 540 in resolution. We used 8-inch screens (NIX™ Pro-Series 8" digital photo frames) to play the stimuli.

There were two types of stimulus sequences. The stranger stimuli were collected in September 2011 and contained 10 bonobos (5F:5M) from the Columbus Zoo at Columbus, Ohio, USA. The subjects had never met or seen these bonobos, except that two Columbus bonobos (Neema and Toby) were also present in the yawning stimuli in the experiment 1. The groupmate stimuli were collected in October 2011 and contained 10 clips of bonobos (5F:5M) from the subject's own social group. For the subject who was also included in the stimuli, we replaced its clip with that of another sex-matched bonobos from its cohort. The two sequences were matched in regard to presentation order, sex and age group. In each sequence, the male clips included four adults and one infant, and the female clips included three adults and two juveniles. The presentation order of the clips in each sequence was always the same, starting with a clip of an adult male and alternating between male and female stimuli each trial. One extra clip of an 11th bonobo from each group was created for the choice introduction phase (see Procedure).

Setup

In this experiment, the subjects could choose two options, an instant option and a delay option. We used two sliding tables to present the options in front of the mesh of the testing room. The distance between the two options was approximately 1.5 meters, except that for one subject (Malayika). For Malayika, the distance was only 0.9 meter due to the limited meshed area in her testing room. The instant option had a black bookstand with two small dices of apple in the front. The delay option had two screens attached to a bookstand by Velcro in a back-to-back way and six apple dices in the front. The front screen served as a preview screen showing a static shot of the video stimulus. The rear screen was playing the video stimulus repeatedly and would be turned to the subject if this option were chosen.

Procedure

Subjects were tested in two conditions, the stranger condition and the groupmate condition. Each condition was administered in one testing day (i.e. two testing days per subject). In each day, subjects started with a choice introduction phase and then proceeded to the test phase.

Choice introduction phase. This phase was designed to introduce the instant option and the delay option to the subjects. The experimenter (E) set up the two sliding

tables but only placed one option in each trial. E first centered the subject, placed the device on the designated table, showed the food pieces to the subject, placed the food in front of the device, and pushed both tables forward. In this 10-trial phase, E presented each option to the subjects five times and they could have 30 seconds to "choose" the option. All five trials with the delay option were playing the same extra clip of the 11th bonobo from the corresponding group. The types and the locations of the options were counterbalanced across trials.

Test phase. Immediately after the choice introduction, the subjects received 10 test trials. These trials were identical to the introduction trials except that 1) both options were present and 2) the stimuli of the delay options were different in every trial. The locations of the options were counterbalanced both within and between subjects.

Coding and analysis

After E pushed the sliding tables forward, a *choice* was coded when the subjects 1) placed their fingers through the mesh in front of the table with an option, or 2) moved their bodies from the center to sit in front of that table. A trial was re-run if 1) the subjects did not made a choice, 2) they were distracted when E was baiting the rewards, or 3) they made a choice before E pushed the tables. A second coder blind to the hypothesis and the testing conditions coded 28.5% randomly selected trials (Cohen's kappa = 1). All stats were two-tailed.

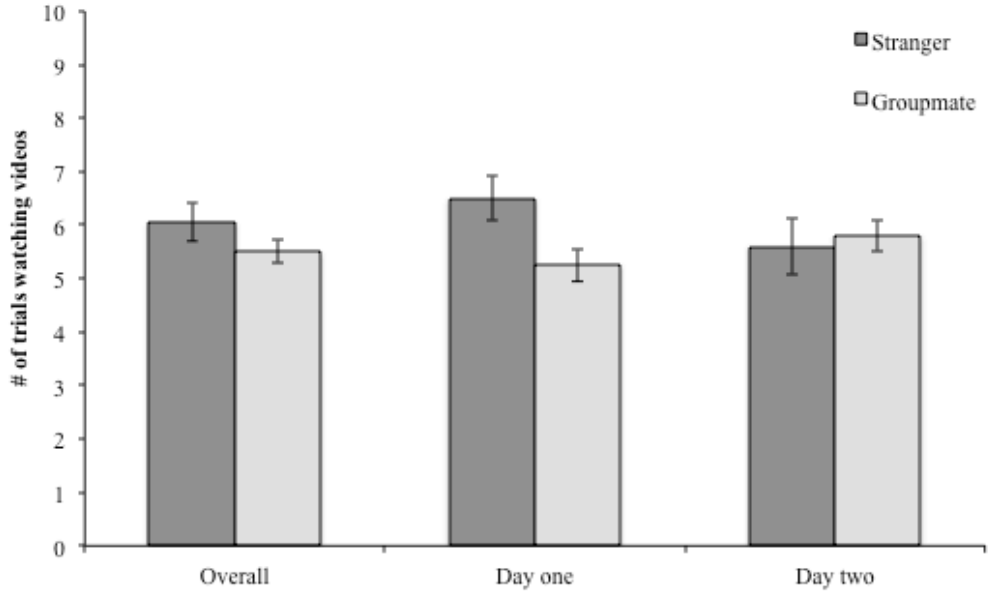


Figure 2.3.3 Results of experiment 2

Results

Figure 2.3.3 shows the results of the experiment. Subjects preferred the delay option to the instant option in both conditions (stranger: $N = 20$, $Z = 2.447$, $p = 0.014$; groupmate: $N = 22$, $Z = 2.021$, $p = 0.043$, Wilcoxon test, two-tailed). We conducted a 2 (membership: strangers versus groupmate) × 2 (target sex: male versus female) repeated measures ANOVA with subject sex as between-subject variable. The analysis revealed overall subjects did not choose to watch the stimuli more often in the stranger condition than in the groupmate condition ($F_{1,18} = 3.020$, $p = 0.099$). An interaction between membership and subject sex was also found to be marginally significant ($F_{1,18} = 4.349$, $p =$

0.052), showing that male subjects were likely more xenophilic than female subjects. The analysis also yielded a main effect of target sex ($F_{1,18}$ = 4.878, p = 0.04), showing that subjects chose the delay option more often when the target in the video clip was a male. In addition, we found significant interaction between target sex and subject sex ($F_{1,18}$ = 5.902, p = 0.026) and a membership × target sex × subject sex interaction ($F_{1,18}$ = 7.624, p = 0.013).

Pairwise comparisons found a difference between two testing days. Subjects did not show an overall xenophilic preference (N = 20 (six ties), Z = -1.64, p = 0.101, Wilcoxon test, two-tailed). However, they were xenophilic on the first testing day, while they showed no preference on the second day (day 1: N = 22, U = 31.5, p = 0.05; day 2: N = 20, U = 49, p = 0.937, Mann-Whitney U test, two-tailed).

Subjects showed a xenophilic preference when the targets were males but not when they were females (male targets: N = 20 (nine ties), Z = -2.138, p = 0.033; female targets: N = 20 (six ties), Z = -0.474, p = 0.635, Wilcoxon test, two-tailed).

Male subjects showed a xenophilic preference (all targets: N = 10 (two ties), Z = -2.209, p = 0.027; male targets: N = 10 (six ties), Z = -2.000, p = 0.046; female targets: N = 10 (three ties), Z = -1.933, p = 0.053, all Wilcoxon test, two-tailed). In contrast, female subjects did not show any xenophilic preference (all targets: N = 10 (four ties), Z = -0.108, p = 0.914; male targets: N = 10 (three ties), Z = -1.265, p = 0.206; female targets: N = 10 (three ties), Z = -1.890, p = 0.059, all Wilcoxon test, two-tailed).

Discussion

The first result was that in both conditions bonobos were more willing to choose the 60-second delay option. The current design is thus validated by replicating the findings of Rosati and colleagues (2007).

The second result of the social valuation task was the presence of xenophilia. Although the overall comparison showed that the subjects had no preference to watch videos of strangers and groupmates, they were indeed xenophilic on the first testing day and this preference quickly disappeared on the second day. These results suggest that subjects were more willing to wait for food when they could watch videos of strangers than when the videos were about groupmates. In support of the first impression hypothesis, videos of strangers are positively valenced so that bonobos voluntarily choose to pay an opportunity cost (i.e. time) to watch them.

It is arguable that the observed xenophilia merely suggests that the subjects were more attentive to the stranger videos. Instead of having higher positive valence, the stranger videos elicited higher arousal. For example, in the chimpanzee results by Campbell and colleagues (2011), yawning was only contagious among groupmates, but their subjects spent more time watching the stranger videos. This is an unlikely interpretation because attention was not free in the current experiment. Watching a video was an economic decision with cost and benefit consequences: the subjects were

willing to pay the cost (i.e. time) in exchange of the food reward *plus* the added value from the video.

In addition, future studies that increase the delay might be able to detect a stronger xenophilic effect. Bonobos on average will become indifferent to one unit of immediate reward and three units of delayed reward if the delay lasts 74.4 seconds (Rosati et al. 2007). As a result, subjects in all conditions were expected to prefer the delay option under the current 60-second waiting period. A longer delay (≥ 74.4s) will thus increase the sensitivity to detect variance in future studies.

Another notable finding is the sex effects of the subjects and the targets. Male but not female subjects were xenophilic, and male but not female targets elicited xenophilic preference. Finally, the current findings show that bonobos are capable of recognizing individual features (membership and sex) in the videos. Therefore, these results suggest that the presentation method in experiment 1 was salient enough to convey information of the targets' group affiliation (and even sex).

2.3.4 General discussion

Overall the two experiments yielded converging evidence that bonobos attribute positive valence to completely unknown strangers. In experiment 1, bonobos showed contagious yawning with strangers. Among adults, the strangers' yawns were likely *more* contagious than the yawns of the groupmates. Because contagious yawning is an indicator of social affiliation in bonobos (Demuru & Palagi 2012), the presence of

contagious yawning among strangers suggests that bonobos by default have a positive appraisal when seeing the strangers. Experiment 2 supports this finding in a social valuation paradigm. When presented with a choice between a small, immediate reward and a large, delayed reward, bonobos were more willing to wait when they could watch a video of a stranger during the delay than when the video showed a groupmate. This xenophilic preference suggests that the stranger videos have higher added value than the groupmate videos. Moreover, the strangers in both experiments were completely unknown to the subjects. Unlike previous studies in which strangers were from neighboring groups (Hare & Kwetuenda 2010, Tan & Hare 2013), our subjects could not have used any visual/vocal communication to form an impression of the strangers prior to the tests. Therefore, the current results provide converging and solid evidence of the first impression hypothesis stating that bonobos have a positive appraisal of encounters with strangers, i.e. bonobos are xenophilic.

Contagious yawning was unlikely a stress response caused by perceived threats from canine displays in the yawning videos. Although yawning behavior exposes canines, it is not a signal of threat because it is not followed by aggression and it occurs mostly in contexts unrelated to aggression and stress (Baenninger 1997, Dobson 2010). Importantly, our yawning stimuli were collected in peaceful, resting contexts. Neither can an incapability of individual recognition explain the yawning results because the social valuation task illustrates that subjects were able to recognize social affiliation from

the videos. Finally, it is unlikely that the xenophilic preference in the social valuation task is a result of arousal and it does not reflect valence. This is because subjects had to make an economic decision between options with differential values, i.e. valence is intrinsic to the choice. We predict that future studies should find a stronger effect in both tasks if there is a longer interval between two testing days to minimize subjects' habituation. In addition, using a longer delay (i.e. ≥ 74.4s) in the social valuation paradigm should allow a greater sensitivity to detect xenophilic preference (Rosati et al. 2007).

The two different paradigms also reveal that xenophilia might be driven by multiple psychological processes (Fazio & Olson 2003, Nosek 2007). In experiment 1, xenophilia was revealed by a stereotypic behavior that is subject to limited voluntary control (Provine 2005). In experiment 2, xenophilia was revealed by a voluntary choice driven by economic decision-making processes (Rosati et al. 2007). Similarly, although bonobos are sensitive to the costs and the benefits when sharing their own food with strangers, their prosociality is not completely strategic because they spontaneously help strangers even when they do not receive any immediate benefits (Tan & Hare 2013). Therefore, it is likely that xenophilia is not just a strategic behavior based on deliberative cost-benefit analysis. It is also subject to a more automatic process that is potentially regulated by rapid physiological responses (Carter & Porges 2010). Future studies will need to determine whether this two-process system can help explain why in some

contexts bonobos treat strangers and groupmates equally, but in other contexts they show a preference for strangers over groupmates. Another line of future research should investigate the psychological and physiological nature of the two processes. For example, emotional responses (Preston & de Waal 2002, de Waal 2008) and oxytocin (Carter & Porges 2010, Taylor et al. 2000) will be expected to be involved in these processes.

Comparison of our bonobo experiments and the chimpanzee experiment also lend support to the phylogeny prediction of the first impression hypothesis. Bonobos but not chimpanzees yawn with strangers (experiment 1, current study; Campbell & de Waal 2011). As discussed above, even when the major methodological differences between the two studies (i.e. potential order and age effects) are controlled, there is still a species difference. It is important for future studies to quantitatively compare the two species in the contagious yawning and the social valuation paradigm. Nevertheless, the current results corroborate the growing literature showing chimpanzees are xenophobic while bonobos are xenophilic (Furuichi 2011, Hare et al. 2012, Herbinger et al. 2009, Tan & Hare 2013, Wilson et al. 2001, Wrangham 1999). These distinct responses to strangers support the phylogenetic prediction of the first impression hypothesis: tolerance and prosociality toward strangers should evolve in a species that has relatively relaxed constraints on sociality (low risk of intergroup aggression/reduced feeding competition). Xenophilia is thus a psychological adaptation to establish a new social relationship

(Porges 2003, Carter & Porges 2010, Taylor et al. 2000). To further test this prediction, it is necessary to conduct pairwise comparisons of closely related species that differ in the intensity of intra-/inter-group competition (e.g. African mole-rats, Ganem & Bennett 2004; macaques, Thierry 2007).

Finally, xenophilia might also have evolved in humans as a psychological prerequisite for prosociality toward strangers. Although in humans strangers' yawns are the least contagious relative to the yawns of groupmates with a positive relationship (acquaintances, friends and kins, Norscia & Palagi 2011), the strangers' yawns are indeed contagious (Anderson & Meno 2006, Giganti & Ziello 2009, Haker et al. 2009, Helt et al. 2010, Provine 1986, 2005, Platek et al. 2003, Senju et al. 2007, Schurmann et al. 2005). It also remains unclear whether humans will yawn with groupmates with a negative relationship. Similarly, it is a well-established phenomenon that humans generally favor ingroups over outgroups (e.g. Hewstone et al. 2002), but the "ingroups" are usually also strangers. Based on current evidence, human interaction with strangers likely results from an interplay of multiple psychological factors including xenophilia and intergroup bias.

3. General Discussion

3.1 Introduction

This dissertation tests two evolutionary explanations for prosociality toward strangers. Across different cultures and early in development, humans spontaneously engage in prosocial behavior toward strangers (e. g. Henrich et al. 2005, Warneken et al. 2006,2007). The parochialism hypothesis suggests that prosociality toward strangers is an adaptation to group-level competition sustained by human cultures and warfare. It further predicts that this prosociality is unique to human, can only be driven by unselfish motivation and encounters with strangers from outgroup should cause a negative appraisal. In contrast, the first impression hypothesis proposes that this prosociality functions to extend an individual's social network. This hypothesis predicts that prosociality toward strangers can evolve in nonhuman species if the benefits of extending social network outweighs the costs. In this case the prosocial motivation can be either selfish or unselfish and encounters between strangers will by default create positive valence as strangers appraise each other.

3.2 The supports for the first impression hypothesis

This dissertation provides support for the three core predictions of the first impression hypothesis. In support of the phylogeny prediction, two sets of experiments reveal that prosocial behavior toward strangers is not unique to humans. Bonobos can be prosocial toward strangers. In support of the motivation prediction, xenophilia does

not require unselfish motivation. Bonobos were motivated by both selfish and unselfish motivations when exhibiting prosocial behavior toward strangers. Finally, in support of the appraisal prediction, two different measures reveal that bonobos by default attribute positive valence to the video stimuli of strangers.

3.2.1 Bonobos are prosocial toward strangers

Study 1-2 reveal that bonobos show voluntary, prosocial behaviors toward strangers in two different contexts. In a food-sharing paradigm, bonobos chose to release a stranger to share monopolizable food. In an instrumental helping paradigm, bonobos sacrificed playing time and energy to help a stranger acquire out-of-reach food. These results are the first experimental evidence that a non-human primate will intentionally act to benefit a stranger. They also contradict the uniqueness prediction of the parochialism hypothesis and instead support the phylogenetic prediction of the first impression hypothesis.

A series of controls demonstrate that the observed prosocial behavior is voluntary and is not explainable by a number of low-level explanations. First, subjects all passed necessary pre-tests to demonstrate an understanding of the different setups in each experiment, so they understood the consequences of their behaviors when they released another bonobo. Second, they were able to inhibit the target behavior (removing the key or pulling the rope) when this behavior did not benefit the strangers. This suggests that they either did not find key removal or rope pulling intrinsically rewarding in this

context or that they could inhibit this response. Third, the bonobos did not show any temporal change in the frequency of prosocial behavior during the experiments. This again suggests that subjects understood the task and did not "mistakenly" open the door and then learn to inhibit this response during the test session. Finally, the subjects were never forced or harassed by the recipient to be prosocial. This further demonstrates the voluntariness of the observed prosociality.

3.2.2 Prosocial motivation is both selfish and unselfish.

Study 1-2 also reveal two distinct proximate motivations underlying this observed prosociality toward strangers. One motivation is other-regarding. Bonobos pulled a rope to help strangers obtain out-of-reach food without gaining any immediate, tangible rewards. In this context, subjects could not receive selfish benefits through kinship, reciprocal exchange, sexual behavior, grooming, or the social reward of physically interacting with strangers. Instead, subjects paid a cost to perform the prosocial behavior because they sacrificed energy and playing time. Given that subjects have shown inhibitory control over rope-pulling as well as an understanding of experimental setup, this helping seems to be driven by an unselfish motivation to benefit the recipient. This result further challenges the uniqueness prediction of the parochialism hypothesis because such other-regarding motivation toward strangers would not be expected to exist in a nonhuman species without intense intergroup competition.

However, it is the finding of the second, selfish motivation that supports the

motivational prediction of the first impression hypothesis. Bonobos were willing to forgo monopolizable, desirable food if they could release a stranger into the room and eat together. This sharing disappeared once sharing did not result in a direct physical interaction with the stranger. This result shows that prosocial actors can indeed obtain selfish benefits from strangers. Instead, a physical interaction with a stranger itself is rewarding enough for subjects to forgo monopolizing highly desirable food.

This result becomes more intriguing given that a physical interaction with groupmates does not seem to motivate bonobos to forgo food in their possession. It is true that bonobos are highly tolerant in the context of feeding, as two bonobos are able to co-feed on a pile of food (Hare et al. 2007, Wobber et al. 2010a). However, when the food is in their complete possession (i.e. sharing can occur only if the possessor actively recruits the recipient or delivers the food), they become reluctant to share with groupmates. Study 1 and at least two other studies with different paradigms have found that bonobos avoid sharing food *in their possession* with groupmates (Sullinger et al. 2012, Jaeggi et al. 2011). This selectivity suggests that the social reward is specific to the encounter of strangers. It is possible that this first encounter represents a critical period to establish a new social relationship. Investing in creating a positive first impression produces higher payoff than investing in a pre-existing relationship that is relatively more difficult to improve. This supports the motivation prediction of the first impression hypothesis – that xenophilia can be selfishly motivated - while directly

challenging the prediction of the parochialism hypothesis that prosociality toward strangers requires unselfish motivations.

3.2.3 Bonobos positively appraise strangers

Study 3 utilized two different paradigms that provide converging evidence in support of the appraisal prediction of the first impression hypothesis: bonobos attribute positive valence to strangers by default. The first task measured yawning, a stereotypic behavior with limited voluntary control (Provine 2005). Contagious yawning has been shown to be a reliable indicator of positive social relationship (social closeness) in various primate species including bonobos (Norscia & Palagi 2011, Demuru & Palagi 2012, Campbell & de Waal 2011, Palagi et al. 2009). This present contagious yawning task shows that adult bonobos spontaneously yawned when they were watching strangers yawn. Moreover, the strangers' yawns tended to elicit more yawns in adult bonobos than the groupmates' yawns did.

In the second task, bonobos evaluated the valence of video stimuli of strangers or groupmates by making voluntary choices. They made an economic decision between a small, immediate reward and a large, delayed reward. The delayed reward was paired with video stimuli of strangers or groupmates. Bonobos showed a stronger preference to wait when they could watch the stranger videos versus a groupmate video. Importantly, watching videos involve a cost-and-benefit trade-off because the two choices had differential rewards (Rosati et al. 2007, Deaner et al. 2005). The observed preference in

bonobos therefore suggests that they attribute a higher intrinsic value to the delayed reward if it was associated with the stimuli of strangers.

Finally, the results of the two experiments combined show that xenophilia is not only driven by a strategic response to obtain social reward (e.g. the social valuation task), but also by a relatively automatic process subject to limited voluntary control (e.g. the contagious yawning task). Therefore, it further shows that bonobos quickly and strongly form positive appraisal of encountering strangers.

3.2.4 Alternative explanations

If these results are valid similar results will be found in future studies testing other populations of bonobos. The observed xenophilia is unlikely a result of the subjects being orphans and living in captivity. The psychological health of orphans was similar to that of the mother-reared bonobos (Wobber et al. 2011). The current findings are consistent with the xenophilia documented in other captive bonobo populations (Holt & van Elsacke 1990, Gold 2001, Pfalzer et al. 1995) and wild bonobo populations (Furuichi 2011). Finally, captivity does not alter chimpanzees' natural xenophobic responses (e.g. Brent et al. 2001, Campbell & de Waal 2011).

A general attraction to novelty and/or risk also cannot explain the current findings. First, bonobos are not neophilic (Herrmann et al. 2011). In contexts where novel humans and novel objects were present and subjects were free to approach and inspect, chimpanzees and orangutans but not bonobos show neophilia by approaching the novel

stimuli more often and faster relative to the familiar stimuli (Herrmann et al. 2011). This lack of neophilia is in a sharp contrast to bonobos' xenophilia when the novel stimuli were unfamiliar conspecifics. Second, bonobos are relatively risk-averse in foraging contexts (Helibronner et al. 2008, Haun et al. 2011). When choosing between a risky reward and a safe reward, bonobos are more likely to pick the safe option than chimpanzees in three different tasks (Helibronner et al. 2008, Haun et al. 2011, Rosati and Hare 2013). Therefore, xenophilia observed in this dissertation is specific to unfamiliar bonobos.

Finally, the strangers used in the current experiments ranged from acquaintances that had been separated in different groups for at least one year, to neighbors that have never been in close physical contacts, to completely novel strangers living on another continent. Bonobos showed consistent xenophilic responses despite various degrees of unfamiliarity. This suggests that xenophilia is indeed a response to unfamiliarity. It argues against the alternative that bonobos just simply remembered past affiliative interactions with the acquaintance or they had already formed a positive relationship with the neighbors via prior visual/vocal communications (see Temeles 1994). Although the current studies did not include the extreme (and artificial) case of unfamiliar, anonymous strangers, the strangers used in the current experiments are of high ecological validity because they resemble natural encounters with strangers in the wild (Furuichi 2011).

3.3 Future studies in bonobos

3.3.1 The boundary of xenophilia

The first line of future research in bonobos should determine the extent and the limit of xenophilia driven by other-regarding and selfish motivations. First, it would be interesting to see if bonobos are also unselfish toward strangers in other contexts. In the instrumental helping task and the prosocial choice task, bonobos show similar level of unselfishness that has been documented in chimpanzees (e.g. Warneken et al. 2007, Melis et al. 2011, Yamamoto et al. 2009, Silk et al. 2005, Jensen et al. 2009). However only bonobos are known to extend this level of unselfishness toward strangers. Similarly, in other prosocial tasks that require other-regarding motivations, chimpanzees will voluntarily help groupmates through tool-transfer (Yamamoto et al. 2012), token-exchange (Horner et al. 2011) and collaboration (Greenberg et al. 2010). Based on the first impression hypothesis, it is likely that bonobos will show other-regard in these tasks toward strangers. Furthermore, the unselfishness in bonobos does not seem to be a response to solicitation/request (see experiment 3 in Study 1). In contrast, several studies show that chimpanzee helping is likely a direct result of solicitation (Melis et al. 2011, Warneken et al. 2007, Yamamoto et al. 2012, but see Horner et al. 2012, Greenberg et al. 2010). Therefore, it is likely that bonobo's unselfishness is comparatively "proactive", especially toward strangers (Jaeggi et al. 2010b).

Second, as shown in the first two experiments in Study 1, bonobos are willing to

forgo highly desirable food in exchange for social reward (i.e. a desirable, physical interaction with strangers). This immediate social reward might facilitate prosocial behavior, because it does not require altruism that is susceptible to cheating and unfairness. Instead, since the actor is rewarded it automatically turns these contexts into mutualism. For instance, distributing the spoils after collaboration is difficult for chimpanzees. Observational studies suggest that sharing clumped resource is mostly passive as a result of harassment or tolerated theft (e.g. Stevens et al. 2004, Gilby et al. 2006, Silk et al. 2013). Experimental studies reveal that successful collaboration hinges upon the divisibility of the reward (Melis et al. 2006, Hare et al. 2007). Except in situations where the partners can negotiate before collaboration (Melis et al. 2010), unequal reward distribution is accepted as the default after collaboration (Hamann et al. 2011, Melis et al. 2011). Another cheater-prone context is the public goods games (Schneider et al. 2012). The first impression hypothesis predicts that higher levels of prosociality would be observed in these contexts when bonobos are paired with strangers in the same room than groupmates .

Third, it remains unclear how much strangers are valued relative to different types of groupmates. The current research shows that bonobos *in general* either prefer strangers to groupmate or at least treat strangers and groupmates equally. However, there are different types of groupmates (e.g. kin, close friends, rivals). A closer look into the pre-existing relationships among groupmates will permit us to more precisely titrate

the default value of strangers relative to different groupmates. For instance, future studies can measure food sharing, instrumental helping and contagious yawning among strangers, ingroup allies and ingroup rivals (see Moore 2009 for an example in human children). Bonobos should show a strong preference for strangers over ingroup rivals, because ingroup rivals are outside the subjects' social network while the strangers are potential social partners. Such preference is expected to be milder if strangers are compared with ingroup allies.

3.3.2 The proximate mechanisms of xenophilia

A second line of future research should identify the psychological, physiological and genetic basis of xenophilia. First, it remains unclear whether the positive appraisal associated with encountering strangers represents a strategic calculation or a more automatic (and probably affective) response. On one hand, a calculating mechanism should be at work to quickly assess if the stranger will become a potential new partner and how "valuable" this particular stranger is. In fact, the social valuation task (in Study 3) and the food-sharing task (in Study 1) suggest that there is a relatively deliberative decision-making process involved in xenophilia because the subjects clearly registered the relative costs and benefits. Theoretically strategic calculation should be more important among strangers than groupmates (Silk 2003, Mills & Clark 1994). Among groupmates, interactants can use a general "attitude" as a heuristic to make quick decision because this "attitude" is formed through numerous previous interactions (i.e.

attitudinal reciprocity, de Waal 2000, de Waal & Brosnan 2005, Schino & Aureli 2010). In this scenario, calculating gains and losses during each interaction is not necessary since the "attitude" is generally a reliable predictor of others' behavior. However, no prior experience exists between strangers, so the interactants will predictably employ a strategic approach to track gains and losses more closely. One reason why calculated reciprocity is rarely observed in studies with nonhuman primates may be because these studies focused on groupmates with stable, pre-existing relationships (Gilby et al. 2010, Gomes et al. 2009, Gomes & Bosech 2009, Melis et al. 2009, Jaeggi et al. 2013, Schino & Aureli 2010). Furthermore, simply pairing strangers together is not enough to generate calculated reciprocity. A recent study paired capuchin monkeys from outgroups in a role-reversal sharing task but found no evidence of calculated reciprocity (Suchak & de Waal 2012). Given that capuchins regularly engage in intergroup conflicts (e.g. Crofoot et al. 2008, Polizzi di Sorrentino et al. 2012), it is not surprising that the calculating mechanism to assess potential new partners is absent in this species. Instead, the first impression hypothesis predicts that such calculated reciprocity might be an adaptation for species to form new social relationships, i.e. it is most likely to be observed in stranger dyads of xenophilic species like bonobos. Similarly the first impression hypothesis predicts that testing bonobo strangers will be a more promising quest to discover other flexible partner-choice/partner-control strategies such as shunning (Melis et al. 2006), image-scoring (Herrmann et al. 2012, Subiaul et al. 2008, Russell et al. 2008),

reputation management (Engelmann et al. 2012), second-party punishment (i.e. the ultimatum game, Jensen et al. 2007, Kaiser et al. 2012, Proctor et al. 2013) and even third-party punishment (Riedl et al. 2012).

On the other hand, a relatively automatic process might be at work to quickly activate the tend-and-befriend response and/or deactivate the fight-or-flight response (Taylor et al. 2000). The presence of this automatic process is evident in the contagious yawning experiment (in Study 3) showing that even the expression of a stereotypic behavior is shaped by the bonobos xenophilic preference. This automatic process has been hypothesized to include an affective component (e.g. emotional contagion, Preston & de Waal 2002, Decety & Svetlova 2012), but future research needs to directly measure affective states to determine 1) whether bonobos experience positive affective states during the encounter with stranger and 2) whether bonobos *share* similar affective states as the strangers. Current approaches to infer affective states in nonhuman animals largely depend on a few explicit facial expressions and behavioral indictors (e.g. self-scratching, chasing, screaming, and behavioral lateralization, Aureli & Schaffner 2002, de Waal 2011, Hopkins et al. 2006). Therefore, future studies can adopt the video-based paradigms in Study 3 and incorporate the manipulation of affective states of the bonobos in the videos. For instance, self-scratching is a well-established indicator of anxiety in nonhuman primates (Maestripieri et al. 1992) and it is also a contagious behavior in humans and macaques (Nakayama 2004, Holle et al. 2012, Feneran et al.

2013). It will be interesting to examine if anxiety is contagious among stranger bonobos. Additionally, the video stimuli in the current social valuation task did not show affective states. They showed bonobos sitting idle with neutral facial expressions. Future studies should systematically manipulate the affective states of the bonobos in the videos (e.g. grooming, chasing or injuries).

The major caveat of relying on facial expressions and behavioral indicators is that it largely limits the feasible measures to a few, mostly negative and dramatic, affective states (Kuczaj et al. 2013). The potential positive affects, which are predicted by the first impression hypothesis, can only be indirectly inferred via the subjects' behavioral contagion and choices. To solve this problem, affective states should be directly measured through physiological responses. However, there are currently no flexible, noninvasive technologies that are applicable to cross-species comparison and capable of direct measurements of "online" physiological responses. One obvious reason is that traditional invasive techniques cannot be applied to animals housed outside of biomedical facilities. Current noninvasive techniques require subjects to remain still while wired sensors are attached to them (e.g. Ueno et al. 2008, 2011, Hirata et al. 2013). Most techniques, including imaging, are not feasible in most non-humans without the use of physical restraint or sedation (Rilling 2008). Finally, most techniques require bulky devices that limit their deployment in any type of "field" context (e.g. zoos, animal sanctuaries or developing countries). To push a much-needed technological

innovation in this field, future studies must be creative to combine the knowledge of primate cognition and neuroscience with the advanced techniques of engineering sciences. One promising technology is nanosensors that can be attached to skin surface. Thomas and colleagues (2011) recently invented a dragonfly-sized physiological sensor that can acquire common physiological indicators of affective states (e.g. galvanic skin conductance, heart rate, skin temperature). Another possible technology is infrared temperature sensors (e.g. remote sensing of nasal skin temperature changes, Kuraoka & Nakamura 2011, Nakayama et al. 2005).

Lastly, future research on the biological basis on xenophilia should extend into the endocrine and genetic levels. Two neuropeptides, oxytocin and vasopressin, and their regulatory pathways should be of particular interests, given that they are shown to assume critical roles in social affiliation in numerous nonhuman species and recently in humans (Taylor et al. 2000, Carter et al. 2008, Carter & Porges 2010, Donaldson & Young 2009, Heinrichs et al. 2009, Insel 2010). On one hand, oxytocin seems to promote prosocial behavior, facilitate establishment of social bonds and reduce stress; on the other hand, vasopressin tends to play a role in mate-guarding and territorial defense (see reviews by Carter et al. 2008, Donaldson & Young 2009, Heinrichs et al. 2009, Insel 2010). To date, only one study has focused on the effect of oxytocin/vasopressin in non-reproductive social behavior in nonhuman apes (Crockford et al. 2013). Chimpanzees show higher levels of urinary oxytocin after grooming with a bonded individual (both

related and unrelated) compared with a non-bonded individual or no grooming at all. Importantly the mere presence of a bonded individual in close proximity does not correlate with higher level of oxytocin. Only grooming, an affiliative physical contact, with bonded individuals correlates with high level of oxytocin. This selective response of oxytocin might underlie xenophilia as well. In particular, the selectivity in Crockford et al. (2013) resembles the result in Study 1 that bonobos shared monopolizable food with strangers (but not groupmates) only if they were able to have physical interaction in the same room.

In addition, the xenophilia observed in bonobos and the unconditional friendliness toward strangers observed in Williams syndrome patients might be homologous (e.g. Meyer-Lindenberg et al. 2006, Santos et al. 2010, Dai et al. 2011). It is true that this comparison remains speculative at the moment. However, the investigation of Williams syndrome is worthwhile because the genomic changes causing this syndrome are known and thus can help identify the genetic basis of xenophilia (Meyer-Lindenberg et al. 2006).

3.4 The ultimate functions of xenophilia

It is impossible to understand the function of xenophilia without comparing bonobos to chimpanzees. The following sections thus start with a brief review of our current knowledge of difference in intergroup behaviors in *Pan*.

3.4.1 Xenophobic chimpanzees, xenophilic bonobos

This dissertation strongly supports that chimpanzees and bonobos have highly divergent intergroup preferences. Bonobos not only groom, co-feed, travel and have socio-sexual behavior with strangers (Hohmann & Furth 2002, Furuichi 2011), but also voluntarily share food with and provide services to strangers (Study 1); chimpanzees avoid, attack and sometimes seek to kill strangers (Mitani & Watts 2005, Wilson & Wrangham 2003, Wrangham 1999; Mitani et al. 2010). Bonobos voluntarily let themselves become outnumbered by two strangers (Study 1); chimpanzees will not approach a stranger unless they hold numerical advantage (Wilson et al. 2002). Bonobos show positive responses and attribute positive valence to the stimuli of strangers (Study 3); chimpanzees inhibit positive responses but show negative responses to the stimuli of strangers (Campbell & de Waal 2011, Wilson et al. 2001, 2007, Herbinger et al. 2009). Bonobos at various ages can be integrated into new social groups quickly and peacefully (1 day, Gold 2001; 14 days, Pfalzer et al. 1994); chimpanzees initiate agonistic responses toward newcomers and successful integration requires extensive familiarization period (app. 17 months, Thunström et al. 2013; app. 4 months, Schel et al. 2013), stepwise or dyadic introduction to avoid power imbalance between the two parties (Baker & Aureli 2000, Schel et al. 2013, Seres et al. 2001), and careful matching of the two parties' age, sex and reproductive status (Baker & Aureli 2000, Schel et al. 2013, Seres et al. 2001, Alford et al. 1995, Brent et al. 1997).

By no means does this contrast suggest an oversimplification that bonobos are

always xenophilic and chimpanzees are always xenophobic. There is definitely considerable intra-specific variation (Chapman & Rothman 2009, Stumpf 2011). For instance, although the agonism has never been escalated to the level observed in chimpanzees, intergroup encounters in bonobos sometimes do lead to tension and avoidance (Hohmann 2001, Hohmann & Furth 2002, Furuichi 2011). Peaceful visits of female strangers *can* occasionally occur between chimpanzee groups (Williams et al. 2004, Emery Thompson et al. 2006, Boesch et al. 2008) and West African chimpanzees appear to have lower rates of lethal aggression toward strangers (Boesch et al. 2008). It is obviously important for future research to investigate the variation of intergroup preferences across field sites, contexts, and even across individuals. However, the existence of intra-specific variation suggests there is certain degree of behavioral plasticity. It does not disprove the inter-specific difference. For instance, relatively low frequency of lethal aggression observed in West Africa chimpanzees is probably because demographic and ecological factors do not allow aggression to escalate (Boesch et al. 2008). In corroboration, although at the behavioral level these chimpanzees seem relatively peaceful, at the psychological level they seem as xenophobic as eastern chimpanzees or captive chimpanzees (Herbinger et al. 2009, Wilson et al. 2001, Kutsukake et al. 2011). Similarly, although it is not impossible to introduce stranger chimpanzees into a new group, it is the difficulty of the introduction process that is indicative of xenophobia in chimpanzees (Gold 2001, Pfalzer et al. 1995, Baker & Aureli

2000, Schel et al. 2013, Seres et al. 2001, Alford et al. 1995, Brent et al. 1997). This problem also highlights the importance of comparative experiments in captivity. Captivity provides a powerful control of the variation in living conditions, meanwhile comparative experiments can minimize the variation in study designs (e.g. see Campbell & de Waal 2010 for a review of numerous versions of contagious yawning design). Therefore, future research should focus on developing creative and ethical paradigms that allow cross-specific comparison of intergroup preference. Two promising tasks are the video-based paradigm in Study 3 and the playback paradigm (Hohmann & Furth 1994, Wilson et al. 2001, Herbinger et al. 2009).

3.4.2 The presence and absence of xenophobia as a result of resource competition

In natural situations, a chimpanzee or a bonobo is mostly likely to encounter three types of strangers: neighbors, immigrants and newborns. The following discussion will primarily focus on the first two types, although it will be interesting to explore the third one given that the oxytocin-vasopressin system is critical to lactation and mother-offspring attachment (Taylor et al. 2000).

Group living is costly and xenophobia is likely a direct result of this cost. A number of socio-ecological factors have been proposed and shown to affect the degree of primate sociality (i.e. group size) including resource competition, predation risk, infanticide risk and disease transmission (Wrangham 1980, Wrangham et al. 1993,

Chapman et al. 1995, Symington 1990, van Schaik & van Hooff 1983, van Schaik 1983, Janson & Goldsmith 1995, Sterck et al. 1997, Freeland 1976, Hart 1990, Loehle 1995, Nunn et al. 2000, Altizer et al. 2003). Among these factors, the primary *cost* of sociality in *Pan* is believed to be resource competition, although the cost of disease transmission will be briefly discussed at the end of the section.

If resource competition is intense and the resource is defensible (Mitani & Rodman 1979, Lowen & Dunbar 1994), selection should favor xenophobia both within group (when the stranger is an immigrant) and between groups (when the stranger is a neighbor). In the case of immigration, the stranger is a new competitor so xenophobia should always be favored except when the philopartic sex can reap the benefit of mating with the stranger. Consistent with this prediction, chimpanzee immigrants (and their offspring) are the frequent victims of aggression led by resident females (Kahlenberg et al. 2008a, b, Pusey et al. 2008, Towsend et al. 2007). On the border, males will attack strange females, but border females are less likely to be victims compared to strange males (especially sexually-receptive females, Willliams et al. 2004). Male chimpanzees will even engage in affiliative and protective behaviors toward sexually mature females probably for the direct benefit of mating (Kahlenberg et al. 2008a, Boesch et al. 2008).

In the case of neighbors, the stranger is a member of a rival group that competes for territory and ultimately for access to resources. Based on Crofoot and Wrangham (2010), intergroup dominance relationships are prevalent in social primates: larger

groups gain priority to access resources. Therefore, xenophobia is also favored by natural selection as a result of intergroup competition. Perhaps xenophobia normally functions to defend the resource from the rival groups. But the extreme form of xenophobia, lethal killing, seeks to weaken the rival group by removing their members (in chimpanzees: adult males and infants, Wrangham 1999, Williams et al. 2004, 2008, Mitani et al. 2010). This xenophobic killing evolves when the injury risk of the aggressors is minimized by the (opportunistic) numerical advantage over the victim (Wrangham 1999, Wilson et al. 2001, 2002, 2012, Mitani & Watts 2005, see also Aureli et al. 2006 for a case in spider monkeys).

However, xenophobia in chimpanzees is not free. The first cost of xenophobia is the risk of injury during aggression. The majority of intergroup encounters end in retreat and avoidance without escalated aggression (Wrangham 1999, Boesch et al. 2008). Lethal killing is only expected to evolve when fission-fusion dynamics creates temporary power imbalance between the two parties (Wrangham 1999). This is supported by the observation that the xenophobic aggressors usually outnumber the victim during intergroup encounters (Wilson et al. 2001, 2002, 2012, Mitani & Watts 2005) and coalitionary attacks against immigrants (Pusey et al. 2008, Towsend et al. 2007, Kahlenberg et al. 2008b).

The second cost of xenophobia is the energetic and opportunity cost, particularly during territorial defense. Chimpanzee males patrol borders frequently (Mitani 2009).

During patrols they sacrifice feeding time and increase travel distance (Amsler 2010). This energetic cost together with the risk of injury potentially create a collective action problem, which might in turn explain why there is individual variation in the willingness to participate in border patrols (Mitani 2009).

The third potential cost is underutilization of border zones. Due to the risk of intergroup aggression, chimpanzees generally avoid the border zone unless they are in larger parties (Emery Thompson et al. 2007, Mitani & Watts 2005, Wilson et al. 2001, 2002, 2012). This risk aversion will predictably lead to the under-use of resource in the border zone (Kelly 2005). Consequently this under-use will intensify within-group competition and deteriorate relationships with groupmates (see Polizzi di Sorrentino et al. 2012 for an example in capuchins). For instance, Kanyawara chimpanzee females establish core areas based on more than just the quality of the area: some border area were rich in resources but remained under-used (Emery Thompson et al. 2007). Alternatively, Wrangham and colleagues (2007) found that border zone under-use was also present in territorial monkeys without risk of intergroup aggression. This provides an alternative that under-use is probably due to the energetic cost of traveling from the core to the border. Still, this work cannot reject the idea that risk aversion leads to under-use of border resources for at least two reasons. First, all three species tested in Wrangham et al. (2007) are territorial and they vary in the risk of lethal killing, the most extreme form of intergroup conflict. Perhaps the under-use was caused by the risk of

intergroup conflict in general. Second, the cost of under-use might be more severe for female chimpanzees, because comparatively high gregariousness in males allows them to travel to the border zone and exploit resources in larger parties, which in turn lowers the risk of being attacked (Wrangham 1999b, Gilby & Wrangham 2008, Langergraber et al. 2009). Furthermore, males move relatively freely across the community range, while females usually limit their activities within a smaller core area that is affected by male's territorial behaviors (Williams et al. 2002).

Taken together, although the proposed costs should be more systematically quantified in future research, this analysis suggests that xenophobia can be expensive. When resources are less limited and/or less defensible, xenophobia should be selected against. This is likely to be the case in bonobos. First, bonobos might have experienced reduced feeding competition given that they might have been living in a richer environment without inter-specific feeding competition against gorillas. Although the nutritional availability of preferred food in one current bonobo field site seems to fall within the range of current chimpanzee habitats (Hohmann et al. 2010), it is possible that the availability of fallback food differs between bonobo and chimpanzee habitats (Marshall & Wrangham 2007). Also the resource distribution might have been much more abundant in the bonobo habitat than the chimpanzee habitat during Pleistocene (Furuichi 2009, Anthony et al. 2007, Plana 2004).

Second, male-male competition for mates is also reduced as the sociality of females

increases (Wrangham 1993, Parish 1996, Hare et al. 2012). A higher proportion of bonobo parties are composed of females compared to chimpanzees (attendance ratio, bonobos: 27%-51%, chimpanzees: 9%-30%, Furuichi 2009). Females even tend to take the leading role in deciding the ranging activity of the party (Furuichi 2011). Unlike chimpanzee females that are rarely observed to bond with each other (Wrangham 2000, Gilby & Wrnagham 2008, but see Langergraber et al. 2009), female-female bonds in bonobo groups are much more common and sometimes even become the most frequent bonds in a group (Stevens et al. 2008, White 1992, Hohmann & Furth 1996, 2002, Furuichi 2011, Surbeck & Hohmann 2008). As a result, a single male bonobo is never as dominant as in chimpanzees and sometimes female bonobos can become dominant or at least co-dominant with males (Parish 1994, White & Wood 2007, Paoli et al. 2006, Furuichi 1997, 2009, 2011, Stevens et al. 2007). This female cooperation, together with the evolution of concealed ovulation (Reichert et al. 2002), is evidence that the dynamics of mating competition in males has been altered in bonobos (Parish 1996, Hare et al. 2012). The aggressive strategy to cooperatively guard and coerce females is no longer effective, as evident by the converging findings that successful male bonobos adopt a friendly rather than aggressive approach (Hohmann & Fruth 2003, Paoli et al. 2009, Surbeck et al. 2012a,b). In other words, for male bonobos their most critical resource becomes indefensible (see also Waller 2011). As a result, selection should disfavor male aggression (Hare et al. 2012). It is important to point out that selection against aggression

should also apply in the context of territorial defense, because ultimately intergroup aggression in chimpanzees is for males to directly or indirectly secure mating success against rival groups (Williams et al. 2004, Boesch et al. 2008). The reduced defensibility of mates might therefore amplify the collective action problem inherent in intergroup aggression and eventually cause this collective defense to break down (Willems et al. 2013).

In sum, the relaxed feeding competition and the indefensibility of mates both might have contributed to the absence of xenophobia in bonobos. Given the costs of xenophobia, selection should favor a more peaceful response toward both immigrants and neighbors. One potential consequence of non-lethal, and relatively non-aggressive interaction with neighbors is that the border zone can be more extensively utilized. Future research should systematically measure if bonobos feed more often in the border area than chimpanzees or if different bonobo group ranges overlap more than chimpanzees. However, it is important to point out that this does not mean bonobos are not territorial or have no constraints on group size. Based on the observation that bonobos indeed have territories and tension can raise during intergroup encounters (Wrangham 1999, Furuichi 2011, Hohmann & Furth 2002), intergroup competition is likely present in bonobos (Crofoot & Wrangham 2010). Given the socioecology of bonobos, direct contest over territories might become ineffective, and the mode of competition might be more accurately described as scramble competition (Snaith &

Chapman 2007).

Finally, it will be interesting to consider the potential effect of disease transmission on shaping the intergroup preferences in *Pan*. Although both species are promiscuous, the frequent socio-sexual behaviors in non-reproductive contexts expose bonobos to a considerable risk of disease transmission (Wrangham 1993, Woods & Hare 2011). In particular, socio-sexual behaviors are frequently observed during intergroup encounters and immigration events (e.g. Furuichi 2011, Gold 2001, Study 1 in this current dissertation). How bonobos respond to this side effect of reduced xenophobia is open to future investigation. Nunn (2003) showed that behavioral (and probably psychological) defense against sexually transmitted disease is likely an ineffective strategy. Therefore, the first impression hypothesis predicts adaptation in the bonobo's immune system to sustain the increased risk of disease transmission (Nunn et al. 2000).

3.4.3 The presence of xenophilia as a result of non-kin cooperation among the dispersing sex

The last section explains that xenophobia is an adaptation to costly group living. When the *costs* of group living are *relatively* low, xenophobia is expected to be reduced or absent. However, this does not explain why bonobos are xenophilic. In other words, we now understand why bonobos are *tolerant* with strangers, but it is still puzzling why they are *prosocial* toward strangers.

In fact, an absence of xenophobia does not necessarily lead to xenophilia. In other

primate species living on highly abundant/indefensible resources, there is evidence that they not only lack xenophobia, but also show no interest in responding to outgroups (e.g. gelada baboons, Bergman 2010; Guinea baboons, Maciej et al. 2013). Interestingly the monkeys in these studies barely engage in any kind of social interaction with those strangers (Bergman 2010, Maciej et al. 2013). Therefore, this pattern suggests that for selection to favor xenophilia, we should consider the *benefits* of group living besides its costs.

Group living has substantial benefits that allow the majority of primates to successfully overcome its costs (Silk 2007). These benefits can be loosely categorized into two types. The first type is risk dilution, which includes predation avoidance (van Schaik & van Hooff 1983, van Schaik 1983, Janson & Goldsmith 1995), infanticide avoidance (Sterck et al. 1997), and takeover avoidance (Pappano et al. 2012). These types of social benefits can generally be obtained through the mere presence of numerous conspecifics, i.e. social interaction rarely needs to extend beyond the basic breeding unit. As a result, an absence of xenophobia is *sufficient* to reap these types of benefits and there should be no selection for xenophilia (see the above evidence of no recognition of strangers in geladas and Guinea baboons, Bergman 2010, Maciej et al. 2013).

The second, and more interesting, type of social benefit is cooperation. This includes coalitionary resource defense (Wrangham 1980, Watts 1998), coalitionary territorial defense (Crofood & Wrangham 2010), cooperative breeding (Clutton-Brock

2002, Kokko et al. 2001), cooperative foraging (i.e. stag hunt, Hare et al. 2007, Tomasello et al. 2012), stress reduction (Abbott et al. 2003, Engh et al. 2006; Sapolsky 2005; Taylor et al. 2000), and commodity trading (Noë & Hammerstein 1994). Unlike the first type, this second type of social benefits requires a differentiated social relationship embedded in a social network. Nevertheless, the problem is still unsolved. The benefits of cooperation do not necessarily result in xenophilia because individuals can reap the benefits with a range of social partners ranging from relatives to reciprocal partners to strangers. According to the theories of kinship and reciprocity, cooperating with strangers will be disadvantageous in comparison to cooperating with relatives or reciprocal partners (Hamilton 1964, Trivers 1971, Wrangham 1980, Silk 2009, Greenwood 1980). Only under special circumstances will strangers become necessary for successful cooperation: 1) strangers are future reciprocal partners and/or 2) the success of cooperation increases as the number of cooperators increases.

Xenophilia is the start of all cooperative relationships

First of all, any social relationship has a start and the start is always among strangers. Recall the three types of strangers that an individual will naturally encounter: newborns, immigrants and neighbors. In most cases, cooperative relationships, either nepotistic or reciprocal, with groupmates develop from newborns (as predicted by kinship theory and reciprocity). As a result cooperation is most likely to occur among

the sex that remains in the natal group (or among them and their mothers), while cooperation among the dispersing sex should be rare (Greenwood 1980).

The male philopatric chimpanzees follow this pattern. Coalitions, hunting, border patrols and other affiliative behaviors are most prevalent among males (Gilby & Wrangham 2008, Mitani & Muller 2005, Mitani 2009a,b). This male-male cooperation is not always among brothers, but it is certainly among males that have known each other for a long time (Langergraber et al. 2009, Lukas et al. 2005). There is also evidence to suggest chimpanzee males do seem to benefit from nepotistic bonds with their mothers by inheriting the mother's home range (Murray et al. 2008). Female bonds are much less common. Even though female-female bonds exist, they are considerably weaker and more variable than male-male bonds, which could be a coincidence of two females ranging in close proximity (Gilby & Wrangham 2008, Langergraber et al. 2009).

In contrast, bonobos present a paradox -- strong female-female alliances in a male philopatric species (Gerlof et al. 1999, Eriksson et al. 2006, Hashimoto et al. 2008). As discussed above, female-female bonds are either the most frequent or the second most frequent bonds, they help females gain dominant/co-dominant status in the social groups, and they drastically reduce male aggression (Furuichi 2009, 2011). To form such strong alliance in a dispersing sex, bonobos must be capable of forming a cooperative relationship with an immigrant. Importantly they do not know each other before they reach adulthood, i.e. the formation of cooperation should be relatively quick. This social

challenge likely provides the selection pressure for xenophilia: an adaptation to quickly include a future partner into one's social network.

To further test this hypothesis, we should systematically compare the ontogeny of non-kin cooperation in chimpanzees and bonobos. In chimpanzees, the first impression hypothesis predicts young chimpanzees will be able to develop a novel relationship relatively quickly, but older chimpanzees will mostly restrict their partner-choice to known partners. Bonobos, young and old, will be predictably easier and quicker to establish cooperation with unfamiliar individuals. Therefore, different developmental trajectories of preference for strangers will be observed between chimpanzees and bonobos. This further raises the question whether the selection for xenophilia indeed acts on the ontogeny of bonobo psychology (Hare et al. 2012). It is likely that bonobos retain the paedomorophic level of stranger tolerance into adulthood, as seen in other psychological traits (inhibitory control: Wobber et al. 2010; memory: Rosati & Hare 2012).

Another prediction is that bonobos will show stronger xenophilia toward individuals who are more likely to become a partner. From the perspective of residents, female immigrants will likely be favored over males. From the perspective of immigrants, their preference might rely more on dominance than on sex because male bonobos can be co-dominant with females and they can receive support from powerful mothers (e.g. Surbeck et al. 2011). Furthermore, immigrants should show stronger

xenophilia than residents given their greater need to affiliate. This mixture of factors might explain why the current dissertation does not show a clear sex effect. (However, it is important to point out that an absence of sex difference will not reject the first impression hypothesis because it only suggests that xenophilia is inflexible.) Future studies should carefully manipulate these factors and create the proper contexts to test these predictions.

If xenophilia evolves through this scenario, this suggests that xenophilia is not a challenge to the reciprocity theory (see also Delton et al. 2011). They are two complementary aspects of non-kin cooperation. Reciprocity provides an explanation to the *maintenanc*e of non-kin cooperation, while xenophilia provides an explanation to the other, overlooked aspect: the *initiation* of non-kin cooperation. Therefore xenophilia and reciprocity likely co-occur in species in which individuals of the dispersing sex frequently engage in affiliative social relationships. Two candidate primate groups are muruiqis (Printes & Strier 1999) and Sulawesi macaques (Riley 2010) that have tentative evidence that the dispersing sex maintains an egalitarian relationship.

Lastly, it remains an open question why bonobos do not evolve female philopatry given the importance of female alliances (Willems et al. 2013). One possible answer is phylogenetic constraints (Thierry 2013).

Strangers increase the chances of success in cooperation

Besides being the initiator of reciprocity, strangers can be necessary when the benefit of cooperation increases as the number of participants increases. First, this numerical benefit can exist in mutualistic cooperation similar to the stag hunt game where cooperation yields a larger benefit per capita that individuals acting alone (e.g. Skyrms 2004, Tomasello et al. 2012). However, currently there remains no research on whether bonobos are capable of playing the stag hunt game although they can solve mutualistic collaborative task (Hare et al. 2007). Second, this numerical benefit can also exist in the case of group augmentation where individual fitness is higher in larger groups (Clutton-Brock 2002, Kokko et al. 2001). As a result, selection should favor behaviors that increase the group size such as cooperative breeding of unrelated infants (Kokko et al. 2001) and perhaps even xenophilia. Third, this numerical benefit might also be found in biological markets because more service providers lead to lower price (Noë & Hammerstein 1994, Fruteau et al. 2009). It is important to point out that the benefits that strangers provide in stag hunt, group augmentation and biological market are not different from the benefits provided by groupmates. As a result, if these cases are responsible for the evolution of xenophilia, it should occur only when there are not enough groupmates and the most effective way to increase group size is through xenophilia. Compared to the research foci on social bonds and reciprocity in bonobos, there remains little interest in applying the frameworks of mutualism, group augmentation and biological market to bonobos.

3.5 The first impression hypothesis in human evolution

3.5.1 The costs and benefits of human xenophilia

By following the same cost-benefit analysis of a new social relationship, we can examine the origin of human xenophilia in light of the first impression hypothesis. It is true that the process of human evolution has multiple stages. Each stage was characterized by its specific ecology and thus had unique selection pressure for sociality (Foley & Gamble 2009). Moreover, the social structures of hominins at different stages remain largely unknown (Shultz et al. 2012). As a result, the following preliminary analysis will mainly focus on some candidate factors that might have contributed to the origin of xenophilia observed in the modern humans (Hill et al. 2011).

First, moving into open habitats increased predation risk and enhanced the degree of fission-fusion, which in turn might have reduced the level of xenophobia. On the one hand, open habitats contained more dispersed and patchier food resources, which increased the need for fission during daytime foraging (Foley & Gamble 2009, Aureli et al. 2008). On the other hand, the high risk of predation would lead to a higher average population density (Hill & Lee 1998) as well as the need for fusion during nighttime sleeping (Aureli et al. 2008). This fission-fusion dynamic might even occur on a daily basis (Aureli et al. 2008). Under this circumstance, the frequent fission-fusion dynamics was a solution to the increased cost of group living (Isbell & Young 1996). Consequently interactions with unfamiliar individuals became more frequent, which might result in

reduced xenophobia. However, as discussed above, co-presence with strangers does not select for xenophilia (see examples of gelada and Guinea baboons, Bergman 2010, Maciej et al. 2013). There must be some social benefits of having a relationship with the strangers to enable selection for xenophilia. It is important to point out that this enhanced fission-fusion dynamics in hominins might be more than just co-presence (Aureli et al. 2008). This type of fission-fusion is homologous to those of bonobo and chimpanzee groups, i.e. the temporal split of a large, structured social group where individuals already engage in rich social interactions. This is in contrast to a loose union of small social units where inter-unit interaction is rare (e.g. folivorous primates living in multilevel societies). In other words, the type of fission-fusion dynamics in hominins probably led to further selection for xenophilia.

Second, as in bonobos, non-kin cooperation provided the social benefits of xenophilia. First of all, where are the strangers from? In bonobos, xenophilia might be a result of cooperation among the dispersing sex (i.e. the strangers are immigrants). However, it remains largely unknown what the dispersal pattern was at each stage of human evolution. There is evidence that autralopiths and Neanderthals followed a *Pan*-like male philopatry system (Copeland et al. 2011, Lalueza-Fox et al. 2011, but see Koenig & Borries 2012). If true, it is not impossible that bonobo-like xenophilia might also be present in these early hominins (i.e. xenophilia in bonobos and humans might be homologous). An analysis of modern hunter-gatherer societies reveals a highly flexible,

bi-sexual dispersal pattern (Hill et al. 2011). Although it remains unclear when this bi-sexual dispersal pattern occurred, it likely contributed to the high proportion of non-kin present in human social groups (Hill et al. 2011). Similarly, we know little about when human-like pair-bonding evolved, but an increased degree of pair-bonding might have further facilitated non-kin cooperation because a female's natal group can bond with a male's natal group via the bond formed between the female and the male (Chapais 2013). In this case, strangers are residents from neighboring groups. Finally, strangers can come from ingroup. As discussed above, the enhanced fission-fusion dynamics likely decreased the familiarity with groupmates (Aureli et al. 2008, Foley & Gamble 2009). Furthermore, population size (or individual social network size) has significantly increased over the process of human evolution (Hill & Dunbar 2003, Dunbar 2008, Gowlett et al. 2012, Shultz et al. 2012). This combination of fission-fusion and large population might have thus generated a new type of stranger that is rarely seen in other primates: ingroup stranger.

The above scenarios suggest that human social interactions with non-kin and even strangers might have become increasingly frequent (Seabright 2012). Meanwhile, at some point humans became obligate cooperators given their increasing reliance on cooperative foraging and cooperative breeding (Kaplan et al. 2000, Hill et al. 2009, Tomasello et al. 2012). In bonobos, non-kin cooperation is mainly limited to female-female alliances (i.e. xenophilia functions to initiate a reciprocal relationship, Hare et al.

2012). We currently have no evidence that bonobo xenophilia contributes to the numerical strength in stag hunt, group augmentation and biological market (see 3.4.3.2). In contrast, given the massive scale of human cooperation, it is possible that in humans the social benefits of xenophilia include 1) initiating a reciprocal relationship (perhaps both between individuals and between groups, Delton et al. 2011) and 2) providing numerical strength to increase the chances of success in the contexts of stag hunt, group augmentation and biological market (Tomasello et al. 2012, Noë & Hammerstein 1994).

Third, as humans became increasingly dependent on technology, a new type of social benefits of strangers occurred: strangers provide novel information and/or materials. Both modeling and experimental works have shown that social tolerance is crucial to successful transmission of social knowledge (van Schaik & Pradhan 2003, Horner et al. 2006, Pradhan et al. 2012). Furthermore, faithful transmission is not sufficient to generate human-like cumulative culture. Cumulative culture requires frequent interactions among social learners that enable the dissemination of cultural innovation; large population density and/or frequent intergroup communication are also necessary to maintain cumulative culture (Shennan 2001, Henrich 2004, Powell et al. 2009, Kline & Boyd 2010). In this case, strangers can offer a unique social benefit, novel cultural knowledge. Additionally strangers might also become transporters of raw materials across territories (McBrearty & Brooks 2000). This social benefit is stranger-

specific, which might in turn provide one of the strongest selection forces for human xenophilia (this is similar to the concept of "weak ties" in sociology, Granovetter 1973).

3.5.2 Xenophilia versus xenophobia in humans

The above discussion shows that human xenophilia can be explained by the individual costs and benefits of starting new social relationships. Is the first impression hypothesis compatible with the observed xenophobia in humans? Humans readily show prejudice (Devine 1989), fear (Olsson et al. 2005), avoidance (e.g. Kinzler et al. 2007) and kill strangers (Hill et al. 2007; Keeley 1996; Wrangham 1999; Walker et al. 2013). This xenophobia develops early in life (e.g. Kinzler et al. 2007) with a biological basis (Harris & Fiske 2006; Hein et al. 2010). There are two important points to consider here. First, the presence of xenophilia in one context does not preclude the presence of xenophobia in another context. This is even the case in bonobos. In the wild intergroup encounters are not completely free of tension (Furuichi 2011, Hohmann & Furth 2002). Following the cost-benefit analysis approach, it is not impossible that xenophobia is favored by natural selection in one circumstance while xenophilia is selected for in another situation. In particular, there are different types of strangers. This highlights the second point. Xenophobia is usually observed 1) in presence of rival/extreme outgroups or 2) in a comparison between ingroup strangers and outgroup strangers. In other words, the major focus of the literature is on one type of strangers who are least likely to become new social partners. The first impression hypothesis actually predicts that these

strangers should not be the recipients of xenophilia. As discussed above, the emergence of ingroup strangers in humans suggests a disassociation between familiarity and group affiliation (i.e. adult strangers are not necessarily from outgroup). Future research should carefully distinguish the different types of strangers and systematically compare them to test under what circumstances human xenophilia evolved. For example, if human xenophilia evolved as a result of strangers being the providers of novel information, we will predict that in the context of social learning, xenophilia should be the strongest when the strangers are from an outgroup.

Appendix A Subject information of experiment 1-2 in Study 1

Name	Sex	Age estimate[1]	Group #	Past study[2]	Experi-ments	Experiment 1		Experiment 2	
						S-G[3]	# of times to release each recipient[4]	Condition-Recipient[3]	# of times to unlock each room[5]
Luozi	M	7	1	No	1-2	*Waka*-Muanda	2-0	G-Muanda	3-2
Mabali	M	7	1	No	1-2	*Waka*-Lisala	5-0	S-*Kinshasa*	1-1
Kasongo	M	8	1	Yes	1-2	*Waka*-Kalina	5-0	G-Kalina	1-2
Dilolo	M	9	1	No	1-2	*Sake*-Muanda	5-0	S-*Kinshasa*	3-0
Matadi	M	10	1	No	1	*Sake*-Kalina	0-0	N/A	N/A
Kikwit	M	12	1	Yes	1	*Kinshasa*-Lisala	0-0	N/A	N/A
Muanda	F	6	1	No	1-2	Kinshasa-Kalina	4-0	G-Kalina	0-3
Lisala	F	9	1	Yes	1-2	*Kinshasa*-Muanda	4-0	S-*Masisi*	1-0
Kalina[6]	F	12	1	Yes	1-2	*Sake*-Lisala	4-1	G-Bandundu[6]	1-1
Masisi	F	4	0	No	1-2	Muanda-Waka	3-2	G-Kinshasa	4-1
Waka	F	4	0	No	1-2	*Kalina*-Kinshasa	1-4	G-Sake	4-1
Sake	F	5	0	Yes	1-2	Muanda-Masisi	0-5	S-*Bandundu*	4-0
Katako[6]	F	6	0	No	1-2	Muanda-Masisi	4-1	S-Muanda	5-0
Kinshasa	F	6	0	No	1-2	Kalina-Sake	0-1	S-*Bandundu*	3-1

1 Age estimates are based on Wobber et al. 2010 and the medical records of Lola ya Bonobo

2 Past study refers to Hare & Kwetuenda 2010

3 S, G stands for stranger and groupmate. Names in italic refer to complete strangers.

4 The first and the second number refers to # of trials where the stranger and the groupmate was firstly released, respectively

5 The first and the second number refers to # of trials where the recipient and empty room was firstly unlocked, respectively

6 Kalina was tested with her dependent infant and Katako was tested with another 3-year-old orphan.

Appendix B Subject information of experiment 3-4 in Study 1

Name	Sex	Age estimate[1]	Group #[2]	Experi-ments	Experiment 3		Experiment 4	
					Stranger[3,4]	Groupmate[4]	Condition-Recipient[3]	# of times to pull the rope[4]
Mabali	M	8	1	3-4	*Sake* (4-1)	Masisi (0-1)	G-Kasongo	0-0
Kasongo	M	9	1	3	*Lukuru* (3-1)	Masisi (6-4)	N/A	N/A
Dilolo	M	10	1	3-4	*Chibombo* (2-3)	Kasongo (1-0)	S-Sake	0-0
Kikwit	M	13	1	3-4	*Chibombo* (1-0)	Mabali (5-4)	G-Waka	0-0
Chibombo	M	4	0	3	*Sake* (5-0)	Lukuru (4-1)	N/A	N/A
Lisala	F	10	1	3-4	*Chibombo* (1-0)	Mabali (3-1)	G-Waka	0-0
Masisi	F	5	1	3	Lukuru (0-0)	Waka (0-0)	N/A	N/A
Waka	F	5	1	3-4	Chibombo (4-1)	Kasongo (6-1)	S-Sake	0-0
Sake	F	6	2	3-4	*Kasongo* (1-1)	N/A	S-*Matadi*	0-1
Katako	F	7	1	3-4	Sake (3-0)	Masisi (4-1)	S-Chibombo	0-0

1 Age estimates are based on Wobber et al. 2010 and the medical records of Lola ya Bonobo.

2 In the year between experiment 2 and 3, Katako, Masisi, Sake and Waka have been transferred to a new group.

3 S, G stands for stranger and groupmate. Names in italic refer to complete strangers.

4 The 1st and 2nd number refers to # of trials where the rope was pulled in the experimental and control condition, respectively

Appendix C Reproductive history of female bonobos from the sanctuary

Name	Estimated Birthday[1]	Date of 1st observed menstrual cycle	Age at 1st menstrual cycle	Date of 1st birth	Age at 1st birth
Bandundu	1/1/97	5/12/06	9	5/22/08	11
Isiro	1/1/98	7/19/06	8	12/7/10	12
Kalina[2]	1/1/98	2/1/06	8	4/25/07	9
Kinshasa[2]	1/1/04	2/27/12	8	N/A	N/A
Kisantu	1/1/99	1/19/06	7	2/26/07	8
Likasi	1/1/01	N/A	N/A	6/17/09	8
Lisala[2]	1/1/01	1/17/10	9	12/4/11	10
Lukaya	1/1/00	1/28/08	8	9/19/08	8
Maya	1/1/93	3/25/03	10	5/22/04	11
Noiki	1/1/99	8/13/08	9	11/21/09	10
Opala	1/1/95	1/7/04	9	10/19/04	9
Salonga	1/1/98	N/A	N/A	1/26/06	8
Sankuru	1/1/02	2/20/10	8	N/A	N/A
Semendwa	1/1/97	3/2/04	7	9/6/05	8

1 Based on the medical records of the sanctuary and Wobber et al. 2010, all were estimated to January 1st

2 Subjects of the current study

Appendix D Subjects in experiment 1 of Study 2

Subject			Recipient				
Name	Sex	Age*	Name	Sex	Age*	Familiarity	Location
Boyoma	M	6	Noiki	F	11	Ingroup	Left
Dilolo	M	10	Lukuru	F	6	Outgroup	Left
Kasongo	M	9	Chibombo	M	6	Outgroup	Right
Kikongo	M	9	Api	M	9	Ingroup	Right
Mabali	M	10	Kodoro	M	4	Outgroup	Right
Maniema	M	8	Kikongo	M	9	Ingroup	Left
Masisi	F	6	Chibombo	M	6	Outgroup	Left
Noiki	F	11	Boyoma	M	6	Ingroup	Right
Sake	F	6	Katako	F	7	Outgroup	Right
Tshilenge	F	7	Muanda	F	6	Ingroup	Left

* Based on estimates from Wobber et al. 2010

Appendix E Subjects in experiment 2 of Study 2

Subject			Recipient			
Name	Sex	Age*	Name	Sex	Age*	Location
Boyoma	M	6	Noiki	F	11	Right
Dilolo	M	10	Mabali	M	10	Right
Kikongo	M	9	Tchilenge	F	7	Left
Kinshasa	F	6	Muanda	F	6	Left
Noiki	F	11	Kikongo	M	9	Left
Sankuru	F	11	Tchilenge	F	7	Right
Tshilenge	F	7	Kikongo	M	9	Left

* Based on estimates from Wobber et al. 2010

Appendix F Subjects in experiment 1 of Study 3

Subject	Sex	Estimated Age[2]	Testing Order[3]	Stranger stimuli		Groupmate stimuli	
				Experimental[4]	Control[4]	Experimental[4]	Control[4]
Api	M	11	S-G	3	1	0	0
Bili	M	10	S-G	4	3	0	2
Bisengo[1]	M	6	G-S	0	0	6	0
Eleke	M	6	G-S	1	0	4	0
Elikya[1]	F	6	S-G	2	4	0	0
Ilebo	M	9	S-G	2	0	4	5
Isiro[1]	F	13	S-G	5	3	1	0
Kalina[1]	F	13	S-G	0	0	3	0
Kananga	F	3	S only	0	0	N/A	N/A
Kasongo	M	9	G only	N/A	N/A	3	0
Kikwit	M	13	S-G	0	0	1	0
Kisantu[1]	F	12	G-S	8	5	2	4
Likasi	F	10	G-S	0	0	2	2
Lisala	F	10	S only	3	0	N/A	N/A
Lomami	M	12	S-G	3	1	0	0
Lukuru	F	5	S only	0	0	N/A	N/A
Mabali	M	8	S-G	1	4	0	3
Malayika[1]	F	4	S-G	3	1	0	0
Manono	M	17	G-S	0	1	0	0
Maya[1]	F	18	G-S	1	0	1	0
Mbandaka	M	9	G-S	7	4	5	3
Sake	F	6	G-S	1	0	12	2
Semendwa[1]	F	14	G-S	4	2	5	7
Waka	F	5	G-S	0	0	0	0
Yolo	M	7	G-S	0	0	0	1

1. Subjects that were tested in pairs

2. Age estimates based on Wobber et al. 2010 and the medical records of Lola ya Bonobo

3. S stands for strangers, G stands for groupmates. Four subjects only had data from the first testing day.

4. The number refers to the frequency of yawns during the 10-min watching phase.

Appendix G Subjects in experiment 2 of Study 3

Subject	Sex	Estimated Age[2]	Testing Order[3]	# of trials watching stranger videos	# of trials watching groupmate videos
Api[1]	M	12	S-G	8	7
Bandundu	F	15	S-G	6	5
Bili[1]	M	10	G-S	5	3
Dilolo	M	11	G-S	3	4
Eleke[1]	M	7	S-G	5	5
Fizi	M	12	G-S	5	5
Ilebo[1]	M	10	S-G	6	5
Kalina[1]	F	14	G-S	3	6
Kasongo[1]	M	9	G-S	7	5
Katako	F	7	G-S	7	5
Kikwit[1]	M	13	S-G	8	5
Kisantu[1]	F	13	S-G	5	5
Mabali[1]	M	8	S-G	8	7
Malayika[1]	F	5	G-S	5	6
Masisi	F	5	S-G	6	6
Muanda	F	8	G-S	6	6
Opala	F	17	S-G	5	6
Sake[1]	F	7	G-S	7	7
Waka[1]	F	6	S-G	8	7
Yolo[1]	M	8	G-S	8	6
Matadi	M	11	G only	N/A	5
Mbandaka[1]	M	10	G only	N/A	5

1. Subjects that were also tested in experiment 1
2. Age estimates based on Wobber et al. 2010 and the medical records of Lola ya Bonobo
3. S stands for strangers, G stands for groupmates. Two subjects only had data from the first testing day.

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Biography

Jingzhi Tan was born on Jan 28th, 1986 in Guangzhou, China. In 2008, he graduated from Peking University (Beijing, China) with a B.S. in Life Sciences and a minor in Psychology. Below are the lists of his publications and awards.

Publications:

- **Tan, J.** & Hare, B. (2013). Bonobos share with strangers. *PLoS One*. 8(1): e51922.

- Hare, B., & **Tan, J.** (2012). What cooperative abilities did we inherit as an ape? In: *The Primate Mind*, F. B. M. de Waal and P. F. Ferrari (eds.). Cambridge, MA: Harvard University Press. pp. 175-93

- MacLean, E., Matthews, L., Hare, B., Nunn, C., Anderson, R., Aureli, F., Brannon, E., Call, J., Drea, C., Emery, N., Haun, D., Herrmann, E., Jacobs, L., Platt, M., Rosati, A., Sandel, A., Schroepfer, K., Seed, A., **Tan, J.,** van Schaik, C. & Wobber, V. (2011) How does cognition evolve?: Phylogenetic comparative psychology. *Animal Cognition*. 15(2), 223-38

- Rosati, A., Herrmann, E., Kaminski, J., Krupenye, C., Melis, A. P., Schroepfer, K., **Tan, J.,** Warneken, F., Wobber, V. & Hare, B. (2012). Assessing the psychological health of captive and wild apes: a response to Ferdowsian et al. *Journal of Comparative Psychology*.

Awards & Grants:

- Graduate Student Conference Travel Fellowship, Duke University, 2013
- Evolutionary Anthropology Graduate Student Mentorship, Duke University, 2010, 2011
- Duke Graduate Student Fellowship, Duke University, 2008-present